SYSTEMATICS AND NATURAL HISTORY OF THE MYGALOMORPH SPIDER GENUS *ANTRODIAETUS* AND RELATED GENERA (ARANEAE: ANTRODIAETIDAE)

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ABSTRACT

A taxonomic section includes a characterization of the family Antrodiaetidae, a key to its three genera (*Antrodiaetus, Atypoides*, and *Aliatypus*), a revision of *Antrodiaetus*, and a preliminary study of *Aliatypus*. The family, except for two Japanese species of *Antrodiaetus*, occurs only in North America. Of the 13 species of *Antrodiaetus*, four are newly described: *A. occultus, A. cerberus, A. stygius*, and *A. apacheeus*. Six new synonymies are recognized. Natural history data are reported for all species of the three genera. Antrodiaetid evolution, with emphasis on geographic variation and speciation in *Antrodiaetus* and *Atypoides*, is discussed.

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INTRODUCTION

In general morphology and behavior *Antrodiaetus* (Figs. 109–112) and the closely related genus, *Atypoides* (Coyle, 1968), resemble the stout-bodied burrowing trapdoor spiders of the distantly related mygalomorph family Ctenizidae. All species construct tubular silk-lined burrows in the ground and prey nocturnally upon invertebrates which wander within reach of the burrow entrance. This entrance is well camouflaged and is closed off by a collapsible silken collar (or a rigid turret). The long-legged adult males abandon their burrows during the mating season and wander nocturnally in search of females. Most species are found in humid well-drained soil in forest or woodland habitats.

Antrodiaetus and *Atypoides* together form a distinct monophyletic unit within the atypoid mygalomorph spider family Antrodiaetidae. The 13 species of *Antrodiaetus* and the three of *Atypoides* exhibit in toto a markedly disjunct geographic distribution with species in Japan, western North America, and eastern North America. The center of species diversity in both genera is in far western North America. These are clearly the dominant (most abundant and widespread) mygalomorph spiders above 35° latitude on this continent.

Taxonomic revisions of *Antrodiaetus* are nonexistant. Many species descriptions, particularly pre-1900 descriptions, are based on immature specimens or tiny samples, lack diagnostic characters, and are poorly illustrated. Misidentifications are common in the literature. Little has been written about the natural history of antrodiaetid taxa. Such a state of affairs is largely due to the relatively simple external morphology and covert behavior of these spiders.

I have based the taxonomic revision of *Antrodiaetus*, like that of *Atypoides* (Coyle, 1968), upon a thorough and objective search for diagnostically useful characters, my primary tool being an analysis of variation of quantitative and qualitative morphological characters. Because I believe that many kinds of nonmorphological data provide useful, often vital, and interesting information about populations, taxa, and their past history, I have also made a start at a comparative behavioral, ecological, and life history study of the Antrodiaetidae. Using both morphological and nonmorphological data, I have discussed the evolution of *Antrodiaetus* and *Atypoides*. Included is a preliminary consideration of the relationship of the only other antrodiaetid genus, *Aliatypus*, to these two genera. It is my wish that this paper will stimulate further interest and continued research on these and related spiders.

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I sincerely thank the numerous other helpful people and institutions that have loaned material for study; these are named in the Methods section. C. W. Sabrosky and Drs. H. E. Evans, W. A. Shear, and A. A. Weaver have provided identifications of parasites, predators, and some prey.

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NATURAL HISTORY

Only three species of Antrodiaetidae—*Antrodiaetus unicolor*, *Antrodiaetus roretzi*, and *Atypoides riversi*—have had more than a few sentences written about their ecology, life history, or behavior. In this section I shall summarize the natural history literature of the family and add original data. Primarily because of my field studies in 1966, we now know much more about *A. unicolor* than any other antrodiaetid. A comparative summary and discussion of the natural history of the family is placed at the end of this section after the separate consideration of each species. An enormous amount of information is still needed before a valuable comparative biological study of the family can be completed. Hopefully this paper will trigger the search for such information.

My observations were made chiefly in the field during the summers of 1966 and 1967, but I also observed living spiders in the laboratory. Most observations on *Aliatypus* species were contributed by Wendell Icenogle. All specimens are numbered and have been placed in the American Museum of Natural History (AMNH) and the Museum of Comparative Zoology (MCZ); the correspondingly numbered field notes have been placed in the MCZ. Data on burrow architecture refer to adult female burrows unless stated otherwise. In the text many localities are represented by italicized letters; these localities are identified in the records section at the end of the appropriate taxonomic species description.

Antrodiaetus unicolor (Hentz)

ECOLOGY

Geographic distribution and elevation range. Centered in the central and southern Appalachian region of the eastern U. S. with peripheral populations as far west as the Ozark region and south to near the Gulf coast (Map 1). 0–6600 ft (0–2000 m).

Habitat. Optimum conditions for *A. unicolor* are found in humid, cool, densely forested habitats with sandy loam soil. Such habitats are abundant and nearly continuous in the dissected terrain of the central and southern Appalachian Mountains and their foothills and westward over the Appalachian Plateau. The densest and largest burrow aggregations are usually found on the inclined surfaces of slopes and banks along ravines, streams, roads, and trails; at the base of rock (particularly sandstone) outcrops; and in other sheltered spots. Hemlock (*Tsuga*) and *Rhododendron* are often good plant indicators of optimum *A. unicolor* habitats. Over the more peripheral portions of the range of *A. unicolor*, one finds only scattered pockets of favorable habitat separated by larger areas of more or less unfavorable (dry, poorly drained, etc.) habitats. Although sandy loam is optimum, burrows also occur in other soil types, even sometimes in clay soil, decaying logs, etc. Burrows are normally uncommon in rocky, shallow soil that is too well drained.

Within favorable habitats burrows tend to be aggregated where the soil is constantly humid (at least around the lower portion of the burrow) and protected from erosion and flooding. In dry regions burrows are often clumped only near springs, along stream banks, or near seeps at the bases of rock outcrops. Burrow aggregations are seldom found on near-horizontal ground, unless such ground is well sheltered under something such as a rock outcrop, a sandstone shelter cave, or the base of a large tree. Two limiting factors that may contribute to this clumping under shelters are the temporary localized flooding and the buildup of fallen leaf cover on open noninclined ground surfaces. Such flooding and (usually) leaf litter accumulation do not occur on the steeply inclined slopes and banks where *A. unicolor* burrows are common. On these inclined surfaces, burrows are clearly aggregated in stable spots where erosion is minimal, e.g., moss covered areas and bare parts of the bank sheltered under the overhang of ground surface vegetation, exposed rocks, logs, large roots, and tree bases. Branson and Batch's (1968) statement that *A. unicolor* "lives in burrows mostly beneath fallen logs and deep litter" is erroneous.

Population density. The densest and largest populations were found at *C, D, I, J, K, O, P,* and *Q* within the central and southern Appalachian region. Even at such favorable localities, the population consisted of dense aggregations in optimum habitat spots and scattered individuals in intervening areas of less suitable habitat. One of the densest such burrow aggregations covered an area of about 50 m^2 and contained an estimated 80 to 100 adult females and several thousand immatures. Small dense aggregations were common within the larger aggregations in the above localities. A 0.1-m^2 area at *O* contained four brooding females and 25 immatures. An 0.81-m^2 area at *P* contained three adult females and 198 immatures. A 225-cm^2 area at *B* contained two adult females and 31 immatures. In many dissected regions the populations are concentrated and essentially continuous throughout the interconnecting ravines, young valleys, and coves, with the surrounding matrix of dryer ridges and upland areas very sparsely populated. In the peripheral portion of the *A. unicolor* range, aggregations are (like the favorable habitat) discontinuous and generally smaller and less dense.

Associated burrowing mygalomorph spiders. Throughout most of its range, *A. unicolor* is clearly the most abundant mygalomorph spider. Except for areas of overlap with the northern *Antrodiaetus robustus* (Map 1), only in southern and western parts of its range (in lowland habitats and in the Ozark region) is the abundance of *A. unicolor* equaled and sometimes surpassed by other burrowing mygalomorph species. I have found the following such spiders living side by side with *A. unicolor* at the following localities: *Atypoides hadros* Coyle at *F* (These two species have been found together in other southern Illinois localities by other collectors.); *Myrmekiaphila fluviatilis* (Hentz) at *H, O, R, Q,* and Mammoth Cave, Kentucky; *Cyclocosmia truncata* (Hentz) at *Q, R,* and David Crockett State Park, Tennessee; *Ummidia audouini* (Lucas) at Chickasaw State Park, Tenn.; *Ummidia carabivora* (Atkinson) at *N;* and *Ummidia* spp. at *Q* and Blanchard Springs, Arkansas. At *F, A. hadros* was common but not as abundant as *A. unicolor.* At both *Q* and *R, M. fluviatilis* was common but much less abundant than *A. unicolor.* In one low road bank at *Q, A. unicolor, M. fluviatilis, C. truncata,* and *Ummidia* sp. lived together, the latter two species being rare. At all other localities cited above, the other mygalomorph spiders were very rare. *Atypus* species are sympatric with *A. unicolor* but uncommon; I have never observed them at the same locality. I have not found Lycosidae burrows in *A. unicolor* aggregations.

LIFE HISTORY

Males. Males of *A. unicolor* (and all other Antrodiactidae) closely resemble females in external anatomy and behavior until the striking metamorphosis of the final male ecdysis. Only a few obvious, sexually dimorphic characters—a sclerotized lip at the male genital opening, swollen male pedipalpal tarsi, and well-developed seminal receptacles of the females—appear during the later immature instars. The penultimate male undergoes the final molt within its burrow, and the adult remains there without feeding until certain factors trigger its abandonment of the burrow. Upon emergence, it wanders over the ground surface in search of female burrows, mates, and eventually dies.

The data summarized in Figure 1 indicate that the period of male wandering and mating for the entire species population of *A. unicolor* lasts from late July through late December. Because of occasional long-lived males, the mating season may be shorter than the period during which wandering males have been collected. The high frequency of wandering male records during October indicates that this may be the chief mating season of *A. unicolor*. However, all August records of mature males collected within their burrows were from cooler climate localities (*C*, *I*, and *P*) than the October collections and therefore possibly belong to earlier (September ?) emerging populations.

Evidence indicates that within any given local population the time of male emergence (and probably mating) occurs more nearly synchronously and is probably triggered by local climatic conditions. At *N*, J. Berry conducted a systematic, year-long pitfall trap collection resulting in a relatively complete record of male emergence in that population (J. Beatty, personal communication). Traps were put out for approximately 24-hour periods two times each month (only once a month in the winter) in each of 11 different areas. Fourteen of the 18 adult males collected were taken from 22 to 24 October (ten of these on 24 Oct.) following the first heavy rainfall after a dry summer. The other four males were collected on 1 October, 7 November, and 3 January. Pitfall traps maintained continuously from 7 October to 10 November at *E* by J. Nelson several years later (J. Beatty, personal communication) yielded 11 males during the initial week (7–14 Oct.), two the second week, one the third, one the fourth, and none during the final week (3–10 Nov.). A similar pitfall collection maintained by J. Nelson the following year at *G* from 10 September to 2 November yielded the first male during the week 28 September to 5 October, seven males the next week, one the following week, none the next week, and one during the final week (26 Oct.–2 Nov.). Collections during August revealed a pre-emergence synchrony of adult males at localities *C*, *I*, and *P*. Twenty-one of the 22 adult males collected were within their own burrows. I searched hard for wandering adult males during day and night but found only one. It appears that very few males had emerged and that proper conditions could have set off a large synchronous emergence.

A few winter records exist for wandering males of *A. unicolor*—an early January record from *N* and a literature record from *D* of "males observed on [the] surface during late winter" (Branson and Batch, 1968). I have not seen the latter males (from *D*) so only assume that they are *A. unicolor*. Such records are probably either aberrant late emerging individuals or individuals which have extended their above-ground survival time in particularly protective microhabitats.

Females. Pattern of early postembryonic development. Enough data were obtained from stereomicroscopic examination of each preserved *A. unicolor* brood to establish the following pattern of early postembryonic development. Hatching involves the simultaneous (or nearly so) shedding of the chorion and embryonic or "prelarval" (Vachon, 1958) cuticle. The resulting instar, which I shall call the first instar, is the "first free postembryonic stage" of Holm (1954) or "larva" of Vachon (1958). The second instar corresponds to the "first complete postembryonic stage" of Holm (1954) or "first nymph" of Vachon (1958).

The segmentation and appendages of the late embryo, as well as the dark egg teeth, are visible through the chorion. During hatching, first the chorion splits anteriorly and peels back over the abdomen. Usually the embryonic cuticle splits very soon after the chorion and also peels posteriorly, and the chorion and cuticle are shed simultaneously from the posterior of the abdomen and remain attached to each other. Occasionally, possibly because the interval between the splitting of these two membranes increases, they are shed separately. These conclusions about the timing of hatching are based on the following observations of preserved material: 1) Relatively few spiderlings in any hatching brood were actually in the process of peeling back or shedding the chorion or embryonic cuticle, and, in the great majority of those that were, the chorion was either peeling back or was still attached to the spiderling while the embryonic cuticle was peeling back. 2) Almost all shed chorions observed contained the embryonic cuticle.

The embryonic cuticle is very thin and transparent, lacks setae, has blunt nonfunctional chelicerae, and possesses a dark egg tooth at the base of each pedipalp. The first instar (Fig. 4) possesses several tarsal setae, lacks a rastellum or fang on the chelicera, lacks spinneret spigots, has anterior lateral spinnerets, and lacks pigmentation, except for that which slowly develops around the eyes. The second instar (Fig. 5) has functional chelicerae and spinnerets and can locomote rapidly. The chelicerae possess a few rastellar macrosetae and fully formed fangs, the anterior lateral spinnerets are lost, the other two pairs of spinnerets possess spigots, setae are plentiful, and the body is pigmented.

This pattern of development is the same as that described for *Ischnothele karschi* (Dipluridae) by Holm (1954) and for *Atypus karschi* (Atypidae) and *Heptathela kimurai* (Liphistiidae) by Yoshikura (1955, 1958). It is considered by Holm (1954) to be the most primitive pattern in spiders. Vachon (1958) reviewed these studies and is in agreement on the similarity of patterns in the above three species.

Timing of brood development. The numerous field collections of *A. unicolor* broods yield substantial data on the timing of brood development in nature within the species population as a whole. As shown in Figure 2, the egg stage is found from late June to mid-August, the first instar from mid-July to mid-September, and the second instar from mid-August through at least December. The relatively small number of broods in the process of hatching and molting is apparently a result both of the brevity of hatching and ecdysis in individual spiderlings and of the close synchrony of development within each individual brood. The regular temporal pattern of the brood stages and the absence of more than a single brood in the burrow of any brooding female strongly indicate that *A. unicolor* produces only one brood per year in nature. As Table 1 shows, brood development is not strictly synchronous within a local population, populations *C* and *O* showing the largest amount of variation. These data also indicate little or no lag in timing of brood development at warm climate localities (*N*, *O*, *Q*, *R*) behind that in cooler localities.

Substantial evidence indicates that the spiderlings overwinter in the second instar within the maternal burrow and disperse in the spring. As indicated in Table 1, 15 brooding females were collected between 14 September and 3 December from three localities. Each brood consisted entirely of second instar spiderlings, and none of the broods appeared to be diminished. In the December collection from *Q*, the spiderlings were quite sluggish as a result of the cold weather. During this collection and the September collection at *F*, I searched hard for burrows constructed by second instar spiderlings but the smallest burrows found contained only later instars. Two samples of second instar spiderlings from the December *Q* broods were kept alive at a nearly constant temperature of 12°C. One sample was checked in mid-February and the other in mid-March and both were still 100 per cent second instar broods. These were then released at room temperature into a jar of sand, and they constructed burrows within 24 hours.

Few data exist concerning longevity and the time normally required for an individual to mature. Oviposition to the beginning of the third instar may take nine or ten months. I would estimate at least three or four years from egg to sexual maturity. I have collected two brooding females (384 at Blanchard Springs, Ark., on 11 Sept.; 378 at *F* on 15 Sept.) with new cuticle visible under the old cuticle, thus indicating that females continue to molt after becoming sexually mature and after producing broods. The following evidence indicates that a given female may be capable of producing more than one brood. A number of brooding female burrows were each located in the center of a cluster of homogeneously-sized burrows of small immature spiders. Three of these brooding females (787 at Fort Mountain, Ga., 433 at *Q*, and 448 at *F*) were completely isolated from other large burrows.

Brood size and egg size. The sizes of complete broods collected at different localities are given in Table 2. Brood size statistics for the species as a whole are listed in Table 3. All populations with significant sample sizes show a wide range of variation in brood size and overlap with one another, but the means are often quite different. Table 4 indicates that there is much variation in egg size of *A. unicolor*. Egg size variation within an individual brood is quite small.

BEHAVIOR

Burrow structure. A. unicolor constructs a roughly tubular silk-lined burrow which is widened just below the entrance and at the bottom end (Figs. 6–9). The detailed shape of the burrow, its size, and the thickness of its silk lining vary greatly, depending on the size, sex, and reproductive state of the spider, and especially on soil condition. Tables 5 and 6 show the variation in burrow length and entrance diameter in *A. unicolor*. The latter measurement is more closely related (directly) to body size than is burrow length, which is more influenced by soil conditions. The mean size of penultimate male burrows is markedly smaller than that of adult female burrows, probably because of the smaller body size of the males. Soil with many pebbles, rocks, or roots usually contains crooked and/or shortened burrows. Burrows in hard clayey soil are shorter than those in firm sandy soil. Soil stability (and possibly humidity) appears to have considerable effect on the thickness of the burrow lining. Burrows in loose soil tend to have thicker linings than those of the same population in more stable soil. Usually the upper part of a burrow has the thickest silk lining, this probably being, at least in part, an adaptive response to the relative instability (or low humidity) of surface soil. The rest of the burrow is sometimes only thinly lined with silk. Brooding females (even with unemerged broods) often have thicker burrow linings than adult females without broods. All brooding females at *O* had markedly thicker burrow lining than many brooding females at other localities.

Burrow inclination is strongly correlated with the inclination of the immediate ground surface. The *burrow pitch*—here defined as the angle formed between the mean longitudinal axis of the burrow and the line originating at the entrance and perpendicular to the surrounding ground surface (i.e., the deviation of the burrow from the perpendicular)—of the great majority of *A. unicolor* adult female burrows is 0–15°. Exceptions are often the result of rock or root barriers in the soil. Only one or two burrows sloped upward from the entrance. The probable adaptive significance of such a near-perpendicular burrow pitch is that it removes as much of the burrow as possible from the surface soil, which is structurally and climatically (humidity and temperature) more unstable than the deeper soil layers. This might be particularly important on the steeply inclined banks often inhabited by *A. unicolor* where surface erosion is relatively great. Humidity, structural stability, or temperature gradients are directional cues that might be used in burrow construction.

Occasionally, *A. unicolor* burrows have single, short, dead-end side branches. These are either close to the surface (Fig. 10) or, rarely, at the bottom end. One Y-shaped burrow (389 at *F*) with two entrances was found. Only once have I found a spider in a side branch.

Entrance structure. The silk lining of the burrow is extended above the soil surface to form a flexible collar which is collapsed inward to close off the open end of the burrow (Figs. 11–14, 40–43, 59). This collar is composed of excavated soil particles and materials from the immediate ground surface (such as pieces of twigs, leaves, conifer needles, moss, or just surface soil) held together by silk so that its outer surface is camouflaged and its inner surface silk-lined. The kind and quantity of surface material incorporated into the collar depends on its abundance on the immediate ground surface. When open the collar is more or less erect, and when closed it is roughly flush with the ground surface. The relative height of the collar varies noticeably within populations. Population *O* appears to have collars with the largest height/diameter ratio.

The spider collapses the collar in a bilateral manner by pulling inwardly on two opposing sectors (lateral to the spider), producing a condensation of folding at the two opposing points where these sectors meet. When the burrow entrance opens onto an inclined ground surface, these two points are at the ventral and dorsal sectors of the entrance opening, because of the spider's stereotyped foraging posture orientation. The collar (especially of the larger spiders) is frequently somewhat reduced at these two points, which, if the entrance opening happens to be slightly elliptical, also correspond with the ends of the long axis of such an ellipse. Careless observation of such a collapsible collar by Atkinson (1886) led to his erroneous description: "Each door is a surface of a half circle, is hung by a semicircular hinge, and the two meet, when closed, in a straight line over the middle of the hole. . . . " Unfortunately the majority of subsequent descriptions (Simon, 1892; Comstock, 1912 and 1940; Gertsch, 1949; Kaston and Kaston, 1953; Kaston, 1964 and 1966; Pimentel, 1967) of *Antrodiaetus* burrow entrances are apparently based on Atkinson's inaccurate description.

Under certain conditions, a closed collar may be held shut by a small amount of silk spun over the inside surface of the collar. Such sealing is usually performed before a spider molts. The burrow entrances of brooding females are sometimes similarly sealed. Soil plugs are apparently used much more infrequently to seal the burrow entrance. I have found these soil plugs in only five medium-sized burrows (at *O* and *J*) and one adult female burrow (1115 at *Q*). The immature spiders were molting and the adult female had an egg sac. In each of these, the upper 0.5–1.5 cm of burrow just behind the closed collar was packed tightly with soil (Fig. 8).

Burrow construction behavior. Normally an individual probably occupies and enlarges the same burrow during its entire life span, the burrow site initially being chosen by the second instar spiderling. However, I have collected several medium-sized immatures and one adult female *A. unicolor* on the ground surface away from any burrow and have occasionally observed empty burrows with open collars, no spider remains, and no penultimate male molts. Under laboratory conditions, large immature male and female spiders and adult females are capable of constructing burrows from scratch. These observations indicate that the abandonment of burrows and the founding of new burrows at different sites may not be uncommon in nature.

The following account of burrow construction behavior is based on laboratory observations of ten large immature (male and female) and mature (female) spiders burrowing into humid packed sand; it is incomplete and subject to revision when more detailed observations are completed. The initial step is the construction of a shallow enclosure or cell. Next, sometimes after a period of inactivity, the spider extends this closed cell deeper into the soil until the elongate burrow is formed. Most observations were made on the initial cell construction phase, which lasted from 15 to 30 minutes.

Four rather well-defined behavioral components form cell construction behavior: 1) burrowing, 2) excavating, 3) silk application, and 4) raking. Burrowing consists of pushing into the sand, forcing it apart, and compacting it. An initial depression is made by forcing the palps and first legs into the sand surface. Very soon, however, as the size of the depression increases, the other appendages enter into the burrowing movement. Full-formed burrowing behavior consists of the chelicerae pressing forcibly against the side of the bottom of the depression (or burrow) with the legs flexed over the dorsum of the cephalothorax and abdomen and pressing in the opposite direction against the opposing side of the cavity (Fig. 56). Excavating involves digging sand from the bottom of the depression, transporting it, and releasing it on the soil surface. The chelicerae are elevated and spread apart laterally, and the fangs are extended. These are forced ventrally into the sand, flexed, and then lifted away with the sand held in between. The spider then pivots to reverse its direction and moves up to the top of the cavity. The palps aid in holding the sand in the chelicerae. With its front legs, pedipalps, and chelicerae it reaches out of the cell opening over the soil surface (Fig. 57). It then releases the load by opening its fangs and chelicerae, and pulls away from the load while holding the load against the soil surface with its pedipalps. Silk application includes circular and lateral movements of the abdomen and the entire body (with the spider facing down into the cell) and sweeping movements of the spinnerets (particularly the elongate posterior lateral spinnerets), during which silk is applied to the cell wall and most abundantly to the rim of the cell opening (Fig. 58). In raking, the first legs, the pedipalps, and sometimes the chelicerae and fangs reach out past the rim of the cell opening and pull surface detritus and soil back to the rim of the opening and partially over the opening. This material is often compacted by being pressed against the chelicerae by the first legs and pedipalps. After the spider releases it, it is held in place by silk previously applied to the rim.

Cell construction usually begins after considerable searching behavior in which wandering alternates with mild burrowing, which is usually released by depressions in humid sand. Eventually a series of burrowing movements is repeated in one spot. Burrowing usually continues until a fairly deep depression is formed, and then excavating begins and alternates sporadically with burrowing. The frequency of burrowing decreases, and soon silk application begins and, sporadically, but with increasing frequency, accompanies burrowing and excavating. If it follows excavating, silk is usually applied to the sector of the opening rim and cell wall where the soil load was dropped. When the cell becomes deep enough to contain the spider, raking begins and often follows excavating. Usually only a few instances of raking will suffice to pull the rim of the cell opening shut (or almost shut) and thus end the initial stage of burrow construction.

Burrowing, excavating, and silk application continue during the rest of burrow construction, but the manner in which the load of sand is deposited was quite different in the only two spiders observed after initial cell construction. Instead of being deposited on the ground surface, each load was pressed into the burrow wall just below the top of the closed cell. Apparently the pedipalps held the sand against the wall while the chelicerae and fangs were pulled away, then the sand was pushed into the wall with the rastellar area of the chelicerae. This behavior eventually caused the area around the entrance to bulge outward into a mound. Such internal deposition of soil, if it is normal behavior, would seem to be an effective adaptation for minimizing the exposure of the spider to predation. Collar formation has not been observed.

Atkinson (1886) observed burrow construction behavior in several spiders kept in captivity, and although his description is often difficult to understand, his observations generally agree with those above. He observed too, that after the initial cell is closed over, the excavated soil is deposited and pushed into the wall within the upper end of the burrow. "Dome" apparently refers to the closure over the cell. Atkinson claimed that the spider would apply "viscid liquid" as well as silk to the excavated soil deposited at the rim of the cell opening. It is not clear what he meant by "viscid liquid."

Egg sac structure and position. The egg mass of *A. unicolor* takes the form of a flattened sphere or ellipsoid with a maximum dimension of usually 9–14 mm and a thickness of usually 5–8 mm. Apparently this mass is formed on a portion of the burrow lining which has been thickened with a few additional layers of silk. Several layers or sheets of silk are then apparently applied over the egg mass and hold it firmly against the burrow wall, each sheet larger and attached to the burrow wall slightly farther from the egg mass than the previous sheet (Figs. 6–9). J. R. Tripp, who has recently observed oviposition and egg sac construction in this species, confirms that this is the method of egg sac construction (personal communication). Egg sac silk has the same texture and white color as burrow lining silk.

As shown in Tables 5 and 6, the position of the egg sac in the burrow is quite variable for *A. unicolor.* However, while some population samples exhibit wide variation in egg sac position, others (*Q* and especially *O*) show much less variation and have all egg sacs deep within the burrow. In the populations in which brooding females were often actively feeding (*O*, *Q*, and *R*), egg sacs were well below the surface. It is possible that these two phenomena are adaptively linked, since it is likely that egg sacs near the entrance would be more easily damaged during prey capture than egg sacs attached deep within the burrow. Possible environmental causes should be investigated. All but one of the 101 egg sacs were placed on the ventral sector of the burrow wall. Most egg sacs produced a localized constriction of the burrow lumen, but never so much that the spider could not maneuver past it. In at least most cases this constriction is counteracted, because the burrow is somewhat widened in the vicinity of the egg sac.

Overwintering. On 28 December burrows were observed at *B* on an overcast afternoon (noon temperature = 0°C). Five centimeters of snow lay on the ground except under the shelter of a sandstone wall where most of the burrows were located. The upper 1 cm of the sand soil was dry, loose, and unfrozen; the next 9–15 cm frozen; and below this humid, packed, but unfrozen. No burrows were seen with open collars. Close examination of about 20 small and medium-sized burrows revealed only two entrances sealed inside with silk and none plugged with soil. Four burrows were completely excavated. Two of these had one or two very thin silk septa spun across the narrowed central part of the burrows. Two of the burrows did not extend below the frozen zone, the other two did. All four spiders were quite sluggish but became active after several seconds in my hand.

On the night of 2 December and in daylight the next morning, I observed a burrow aggregation at *Q*. The ground was unfrozen, but the air temperature was 3°C at 9 P.M. and –2°C at 8 A.M. At night, during a light snow and rain, I was surprised to find that most burrows of all sizes were open, and most of these had spiders at the entrance in normal foraging posture. These spiders were more sluggish than usual, however. In the morning (clear weather), a few entrances were still open but no spiders were in the entrances. No sealed entrances could be found. This ability to remain active at relatively low temperatures may contribute to the remarkable success of *Antrodiaetus* in the temperate zone.

Behavior of brooding females and broods. The data summarized in Table 7 show that the broods emerge from the egg sac just before, during, or just after they molt from the first to the second instar. In broods that were emerging when collected, only a few first instar spiderlings (when present) but most of the second instar spiderlings (when present) were found outside the egg sac. Also, in emerging broods and in the few completely emerged broods still with egg sacs, most of the first instar exuviae were found in the egg sac. One exception, 477 at *I*, had these exuviae scattered all over the burrow wall. These data indicate that most emergence is performed by the active second instar spiderlings. There is no evidence indicating how the spiderlings escape from the egg sac or how the egg sac is disposed of. In 59 of the 66 burrows with completely emerged broods, the egg sac was no longer present.

Table 8 indicates that while in some populations (*O*, *Q*, *R*) brooding females with egg sac broods do not seal their burrow entrances and usually continue foraging, in others (*B*, *C*, *J*) they commonly maintain sealed burrows. Such sealing of burrows is in contrast to neighboring contemporary nonbrooding females, which, unless molting, usually kept their entrances unsealed and were actively feeding. How long and for what function such burrows are kept sealed is not known. I was unable to determine whether the sealing of burrows containing emerged second instar spiderlings was initially produced by the adult and thus signifies inactivity or whether it is simply the result of spiderlings trailing dragline silk over the inside of the entrance. At least a number of such brooding females had unsealed burrows and were actively feeding.

First instar spiderlings, extremely slow moving, are sometimes seen moving within the egg sac. Second instar spiderlings are active—they can move quickly in response to stimuli, wander over the burrow wall, and are capable of performing many behavior patterns necessary for independent existence. Several second instar spiderlings released on humid sand in the laboratory constructed individual burrows and assumed normal foraging postures. Second instar spiderlings are capable of spinning draglines and normally appear to do so as they move about. When a brooding female burrow with a closed entrance is first discovered, second instar spiderlings are often found in the upper end of the burrow, but these always retreat to the bottom of the burrow as it is excavated. This may be a photonegative response, but other behavioral controls must be operative in preventing these spiderlings from escaping at night if the burrow entrance is open and the brooding female is feeding (such as at *Q* in September and December). Each of the five broods observed on 2–3 December at *Q* was aggregated in the bottom end of the burrow, several in dense clusters; and all spiderlings were sluggish.

There are no data on whether spiderlings normally feed within the parental burrow before dispersal. An observation of a second instar spiderling which had not yet constructed a burrow but which carried a collembola in its chelicerae, and observations of other second instar spiderlings capturing prey after constructing their burrows, indicate that they are at least capable of feeding before dispersal. Intrabrood cannibalism is possible, but the broods observed in fall and winter did not appear to be smaller on the average than those collected earlier.

Molting behavior. Fragmented remains of one and occasionally two old exuviae were often found to be bound with silk and compacted into the bottom end of burrows. I collected (in July, August, and September) ten immature spiders each with an incompletely sclerotized cuticle and a freshly fragmented exuvia mashed into the bottom of its burrow. Seven of these recently molted individuals had sealed their entrances with silk, and three were discovered by scraping the soil (whether the entrances were sealed could not be determined). Four other immatures (also collected during the summer) were found just after ecdysis; they were much less sclerotized and could not move quickly. These were at the bottom end of their burrows, and the intact exuviae were attached lightly to the ventral sector of the wall of each burrow at one-half to three-fourths of the distance from the entrance to the bottom end. One exuvia was attached with its venter against the burrow wall, and its anterior end heading up the burrow. The orientations of the other three were not recorded. The entrances of three of these burrows (133 at *J*, 951 at *C*, and 747 at Brasstown Bald, Ga.) were sealed with silk, the fourth (355 at *J*) was filled with a soil plug. Another medium-sized immature spider (7040 at *Q*) was excavated shortly before ecdysis, which it underwent within a glass vial kept humid by a moist piece of paper towel. Ecdysis lasted ten minutes. Within four days of ecdysis, the spider had thoroughly fragmented the exuvia and formed it into a compact mass bound together with a small amount of silk.

Twenty-seven burrows of recently molted adult males were excavated. All burrow entrances were closed, but 23 were discovered by scraping the soil surface; whether they were sealed could not be determined. Three of the other four were sealed with silk; the fourth was unsealed. In all but two of these 27 burrows the penultimate exuvia was partly broken up, bound with a little silk, and packed lightly into the bottom end of the burrow. Sometimes this exuvia and the end of the burrow were covered with several thin sheets of silk. The other two burrows each contained a pale unsclerotized male resting motionless at the bottom end of the burrow. In each the freshly shed exuvia was attached—venter against the wall, anterior end heading up the burrow—to the silk lining of the ventral sector of the wall, two-thirds (409 at *F*) and three-fourths (450 at Blanchard Springs, Ark.) of the distance from the entrance to the bottom end.

Apparently, molting behavior in penultimate males and other immatures is similar. In summary, ecdysis usually takes place in a sealed burrow on the ventral sector of the burrow wall in the lower half of the burrow (but above the bottom end). Shortly after ecdysis, the spider moves to the bottom end. After sclerotization reaches a certain point, the spider detaches the exuvia from the burrow wall, breaks it up, and compacts it into the bottom end of the burrow, adding silk. Adult males do not usually fragment the molt as thoroughly or pack it into the end of the burrow as compactly as do females or immature males. The sealing of burrows before molting may help protect the molting spider from predation and may maintain a higher, more constant humidity within the burrow.

Defensive behavior. When spiders in normal foraging posture are disturbed by light, substrate vibration, or prodding with a stick, they sometimes retreat down the burrow without closing the collar or may quickly close the collar, often remaining for a time just below the collar holding it closed. During the later stages of excavating to expose a burrow, one finds most adult female spiders at the bottom end of the burrow in an aggressive defensive posture. The spider faces up the burrow with its cephalothorax reared backwards at an angle to the abdomen. Legs IV and III and possibly II hold onto the burrow wall to anchor the spider. The other legs and pedipalps are raised and spread apart. The chelicerae are also raised and spread apart laterally with the fangs extended. If prodded, the spider strikes forcibly with a sudden downward movement of the cephalothorax and chelicerae. Such a defensive posture within the confines of the bottom end of the burrow limits the approach of an attacker to that part of the spider protected by its chelicerae. Younger individuals and adult males tend to be less aggressive and often do not exhibit such defensive behavior while being excavated. Medium and large spiders will often exhibit similar defensive behavior outside their burrows if prodded.

Predators and parasites. Observations show that females and immature males of *A. unicolor* are preyed upon and parasitized by centipedes, pompilid wasps, acrocerid flies, and mites. Adult males have been collected several times from the ground webs of theridiid spiders.

Four instances of apparent centipede predation have been observed. At Clifty Falls, Indiana, a 50–70 mm long scolopendromorph centipede escaped from a burrow containing a recently killed spider. At *L* a scolopendromorph centipede, *Theatops postica,* was found in a burrow with spider remains. At both *O* and Blanchard Springs, Arkansas, a *Theatops spinicauda* centipede was found in an empty *A. unicolor* burrow. One instance of unsuccessful centipede predation was observed at *C* where a nearly dead *Lithobius forficatus* centipede (lithobiomorph) was found in the burrow of a large immature *A. unicolor.* The centipede had probably entered the burrow through the soil; the burrow entrance was sealed shut.

Twenty-one cases of predation by pompilid wasps have been observed (Table 9). No larvae could be reared to adulthood, thus no specific or generic identification could be made. More than one species is probably involved since variation in cocoon size is great. Spiders with attached eggs or early instar larvae were found in the bottom of their burrows dorsal side up and partially paralyzed. Leg jerking was the chief response to disturbance. The wasp egg was always attached centrally on the abdominal dorsum. Soil plugs apparently constructed by the ovipositing female wasp sealed the spider and larva into some burrows (Fig. 15). Cocoons were usually attached to the burrow wall some distance from the burrow end, where the spider remains were usually found. The hollow usually found in the burrow wall just above the soil plug appears to be the source of the plug.

One tiny, recently hatched pompilid larva and its paralyzed food source from *C* were placed in a narrow glass vial and observed through cocoon formation. Feeding lasted four days. The spider remains consisted of a small packet of compacted spider cuticle. On the fifth day, the larva had moved away from the spider remains. It first spun a loose maze of silk threads between the walls of the tube and then constructed the cocoon within this maze. Cocoon construction took less than 24 hours.

Population *P* was parasitized by the dipteran *Eulonchus marialiciae* Brimley of the Acroceridae. Observations were made on 1 and 2 August. This is presently the only host record for the genus *Eulonchus,* which, because its distribution is otherwise limited to western North America (Schlinger, 1966), and, because it is similar to that of the antrodiaetids, may be an important parasite of other antrodiaetid species. Considering that collected specimens of *E. marialiciae* are extremely rare (C. W. Sabrosky, personal communication), the population discovered at *P* was surprisingly dense. One freshly emerged adult was collected vibrating its wings just inside an *A. unicolor* burrow entrance. One pupa was collected from a burrow and kept for several hours until the adult emerged. Several other burrows were found with abandoned pupal skins and spider remains. A total of about 18 adult acrocerids were seen hovering near *A. unicolor* burrow aggregations.

The adults appeared to fly only during the daytime. The largest aggregation of adults (about 12) formed rather quickly as I was excavating several burrows and hovered close to the ground where I was digging, as if attracted by some chemical released by my digging. Twice I observed adults hovering over and momentarily landing near (or on?) a closed burrow entrance. It is probable that, as in other acrocerids, the first instar larva actively searches out the spider, penetrates the cuticle, and develops as an endoparasite. My observations indicate that the larva, after feeding on the spider in the bottom end of the burrow, climbs up the burrow wall, attaches somewhere above the bottom end, and completes development in this spot. (One pupa and three pupal skins were attached here.)

Immature parasitic mites have been found on 18 adult females from nine different localities scattered over the species range. These were usually attached to appendages as well as to the body proper. It is likely that mite parasites on other specimens have gone unnoticed.

Prey capture behavior. The normal foraging posture of *A. unicolor* is as follows (Fig. 59): The spider is positioned inside the burrow just below the opened collar and faces out the entrance with its pedipalps and first legs extended slightly forward and touching the inner surface of the open collar. Usually the spider's venter is against the ventral-most sector of the burrow wall. Sometimes a spider may be in this posture with the collar only partly opened. Often prey capture behavior is also released in spiders which are positioned farther down the burrow or which have their collars closed. Such individuals, however, appear to respond more slowly to prey stimuli.

Larger immature spiders and adult females usually open their collars and assume the typical foraging posture only in very reduced daylight and in darkness. Younger spiders, particularly the youngest, frequently leave their collars open and often assume the foraging posture during daylight hours as well. The less light (heavily shaded habitats, overcast days, early morning and late afternoon hours) and the greater humidity, the more likely a given spider will be found with an open collar or in a foraging posture. *A. unicolor* is thus primarily a nocturnal feeder with some tendency to feed also during daylight hours, depending upon environmental conditions, age, and probably nutritional condition.

Observations indicate that the prey sensing radius of *A. unicolor* does not exceed several centimeters. Substrate vibration transmitted via the burrow lining and collar is apparently the only stimulus used by the spider to determine the presence and location of prey. This conclusion is indicated by numerous observations (in nature and in the laboratory) of prey capture behavior being released simply by the observer gently vibrating the collar or adjacent ground surface with forceps or sticks, thus eliminating visual and chemical cues. Additional evidence also rules out visual signals. In the typical foraging posture, the spider's field of vision is only a limited inverted cone of space projecting out from the burrow entrance; when the great majority of prey is caught, it has not entered this cone. I have frequently observed spiders within closed collars sensing and capturing ground surface prey. Prey capture is commonly performed in the dark; moreover, the eyes of antrodiaetids are quite small.

Casual observation in nature and in the laboratory, as well as motion pictures of prey capture behavior in lab animals, indicate the following pattern for prey capture behavior. After having determined the approximate location of the prey by tactile stimuli, the spider lunges from the burrow entrance at the prey. Legs IV and, usually, III remain within the burrow anchoring the spider to the burrow wall. The pedipalps and legs I are held out in front of the spider, and legs II also usually leave the burrow. The tarsi and penultimate segments of the pedipalps and legs I contact the prey and hold it against the substrate (Fig. 60). Lateral rows of strong suberect macrosetae on the tarsus and tibia of the pedipalps and on the metatarsus of legs I and II aid in holding the struggling prey and probably also provide important sensory input. Sometimes legs II aid in holding the prey. While the prey is held against the substrate, the chelicerae spread apart laterally, the fangs are extended, and the spider strikes forward and down at the prey with the chelicerae. The fangs contact the prey at two well-separated points (Fig. 61). There may be one to several more such strikes and maneuvering of the prey with the pedipalps and legs before the prey (usually still struggling) is quickly pulled down into the burrow by the pedipalps and legs I (Fig. 62). The spider does not usually close the collar until later, presumably after the prey has been subdued. Sometimes, however, friction of the prey or spider legs against the collar as the prey is being pulled into the burrow partly or completely closes the collar. The time from the beginning of the lunge to the disappearance of the captured prey into the burrow for seven filmed prey captures of seven different spiders ranged from 0.8 to 4.5 seconds, with a mean of 1.8 seconds. The time from the beginning of the initial lunge until contact was made with the prey for four of these spiders ranged from 1/32 to 1/16 of a second.

Atkinson (1886) described the capture of an ant. After detecting the ant, the spider quickly closed the collar, leaving it open only a crack. When the ant crossed this opening, the spider threw open the doors and caught the ant. Such behavior was observed several times, and Atkinson concluded that the spider did not strike until it could see the ant through the opening. That vision actually did play such an important role is doubtful.

Prey composition. Records obtained from prey rejectamenta and freshly killed prey found in burrows in nature indicate that *A. unicolor* is markedly unselective in its choice of prey. It appears to capture and feed upon any arthropod that it is capable of catching and killing (speed, strength, and size of the potential prey probably being important factors) that chances to enter within the prey-sensing radius of the burrow entrance. The prey records in Table 10 indicate that ants and beetles form a large part of this species' diet. This is not surprising considering the abundance of these arthropods on the ground surface. However, thinner-cuticled arthropods are probably more common prey than these records indicate; the rejectamenta records are strongly biased toward such thick exoskeleton forms as ants, beetles, and millipedes which are not as finely fragmented by the spider.

The ants consisted of both formicine and myrmicine species, with the large-bodied formicine genus *Camponotus* common. Numerous beetle families were represented. Three millipede families were found: Parajulidae (five individuals), Xystodesmidae (two individuals), and Polydesmidae (one *Scytonotus granulatus*, one *Pseudopolydesmus serratus*, and two *Pseudopolydesmus* sp.). One of the spider prey was a conspecific male; another was a male *Agelenopsis*. Two phalangids belonged to *Leiobunum*. One wasp was a *Vespula*. In the laboratory, *A. unicolor* readily captures and eats *Porcellio* isopods and *Tenebrio* beetle larvae. Small immatures take wingless *Drosophila*. Identifiable prey ranged in length from about 2 mm to a 16-mm carabid beetle and a 25-mm *Pseudopolydesmus* millipede. It is noteworthy that *A. unicolor* is capable of killing and digesting arthropods (ants, wasps, and millipedes) well known for their stings and/or chemical defenses.

Disposal of prey remains. Exoskeletal remains of digested prey are apparently disposed of in two ways: 1) packed into the burrow wall, 2) discarded on the ground surface outside the burrow. In most burrows, prey rejectamenta is found mixed with a small amount of silk and compacted into the bottom end of the burrow. All except the toughest exoskeletal portions (ant heads and thoraxes; beetle heads, thoraxes, and elytra) are usually fragmented. Sometimes similarily compacted rejectamenta is also present in parts of the burrow wall closer to the entrance. These trash packets possibly mark previous positions of the bottom end of that particular burrow. Some burrows with large amounts of rejectamenta in the bottom end had collembola aggregated on and near the trash.

Occasionally spiders kept in the laboratory disposed of pieces of prey remains by placing them on the soil surface outside their burrows. At least some of these pieces were only partly digested and were decaying; this disposal behavior may be an adaptive response to such decay. Other evidence indicates that prey remains are disposed of outside the burrow: many burrows lack or have very little rejectamenta in their walls; a large amount of fragmented insect cuticle lay on the ground surface in the midst of a dense concentration of burrows at *B*. The periodic excavation to enlarge a burrow and the concomitant disposal of trash packed into the burrow end very likely explain both of these latter types of observations. In summary, the primary method of trash disposal *could* involve two steps: 1) packing the fragmented exoskeleton into the bottom end of the burrow and 2) discarding this compacted rejectamenta on the ground surface during burrow enlargement (or after a sufficient amount of trash collects in the burrow end). Such a method might mean less exposure to predation than would the surface disposal of each prey exoskeleton separately.

Mating behavior. Only a single observation exists on the time of day of male wandering; I collected a wandering male (637 at *P*) on 3 August at 9 P.M. (after dark), 90 minutes after a heavy rain. The mostly digested remains of an adult male *A. unicolor* were found in the burrow of a conspecific female (543 at *I*).

Antrodiaetus robustus (Simon)

ECOLOGY

Geographic distribution and elevation range. Eastern Ohio east through Pennsylvania, northern Virginias, and Maryland (Map 1). 0–1500 ft (0–460 m).

Habitat. I have observed *A. robustus* in only one locality; Caledonia State Park in southern Pennsylvania. Small clusters of burrows were scattered over steep, well-shaded banks on a hillside near a stream in mixed conifer-hardwood forest. White pine and hemlock were dominant near the burrow sites. Most burrows were under the shelter of trees, tree trunks, or exposed rocks and roots, and were as common in spots with a thick surface mat of pine needles as where surface litter was absent. The soil consisted chiefly of firmly packed light tan loam with pebbles.

LIFE HISTORY

Males. The data in Figure 1 indicate that male wandering and mating occur during September and October.

Females. The second instar morphology of *A. robustus* is like that of *A. unicolor*.

Four records (Fig. 2) indicate that the timing of brood development may be similar to that of *A. unicolor.* The presence of a fully sclerotized second instar brood within a parent burrow at Canton, Ohio, on 19 October weakly indicates that broods may overwinter within the parent burrow before dispersing. The sizes of the two completely collected broods are given in Table 3.

BEHAVIOR

Burrow structure. The five adult female burrows observed (Table 6) were similar in structure to *A. unicolor* burrows. They were widened just below the entrance and at the bottom end, and entirely or almost entirely lined with silk. The silk lining was thickest at the upper end. Burrow pitch ranged from 0 to 10°. All burrows sloped downward from the entrance. The burrow of one immature had a dead-end side branch near the bottom end, another immature burrow had a similar side branch near the surface.

Entrance structure. The silk lining of the burrow is extended above the soil surface to form a flexible collar like that of *A. unicolor.* This collar is well camouflaged and is opened and closed in the same manner as that of *A. unicolor.*

Egg sac structure and position. Both egg sacs observed were constructed and positioned like *A. unicolor* egg sacs. Both were in the bottom half of the burrow on the ventral sector of the burrow wall (Table 6).

Behavior of brooding females. Both females with egg sacs (collected near midnight) had their collars closed and sealed lightly on the inside with silk.

Molting behavior. Fragmented exuviae were sometimes found to be bound with silk and compacted with prey rejectamenta into the bottom end of burrows.

Defensive behavior. All individuals in foraging posture at night retreated down the burrow when disturbed by light or vibrations. Adult females and often immatures assume an aggressive defensive posture like that of *A. unicolor.* Both brooding females were particularly aggressive.

Feeding behavior. The foraging posture of *A. robustus* is like that of *A. unicolor.* Individuals assumed this stance (with the collar open) only in twilight and at night. Fragmented prey cuticle (primarily of ants and beetles) was found packed into the bottom ends of most burrows.

Antrodiaetus pacificus (Simon)

ECOLOGY

Geographic distribution and elevation range. The Pacific Coast of North America from San Francisco Bay north to southern Alaska, with outlying, perhaps isolated, populations in the montane areas of western Idaho, northeastern Oregon, and adjacent Washington (Map 2). 0–7500 ft (0–2280 m). The range of *A. pacificus* extends much farther north than that of any other North American mygalomorph spider.

Habitat. The habitat requirements of this species appear to be similar to those of *A. unicolor.* Optimum conditions for *A. pacificus* are apparently found in humid, cool, rather densely forested habitats with deep loam or sandy loam soils. Such habitats are particularly abundant in the moist lowlands and mountains along the Pacific Coast from northern California into Alaska (Fig. 63), but are less continuous inland, there to be found in the mountains of Idaho, eastern Washington, and eastern Oregon.

A. pacificus also occurs in the volcanic "sand" soil of the Cascade Mountain Range, and even constructs burrows in decaying logs in Douglas fir forest. Burrows are sparse in rocky areas with shallow, fast drying soils. The densest aggregations were discovered in soil that was humid and firm at or just below the surface. Within favorable habitats, burrows tend to be clustered in sheltered spots protected from erosion and flooding. Such spots are found on the stable parts of slopes and banks along ravines, streams, trails, and narrow roads. Moss-covered bank surfaces, or portions under the shelter of root, log, rock, or tree overhangs are, as in *A. unicolor*, common sites of burrow aggregations.

The densest and largest population was found at *I* where one burrow cluster contained four adult females, one adult male, and 36 immature spiders within 0.25 m^2. The largest and densest population in the eastern part of this species' range was found at *U*.

LIFE HISTORY

Males. The data in Figure 1 indicate that male wandering and mating occur between early June and early November, with peak activity perhaps from late July to late September. Records from a few relatively well-collected localities hint that, as in *A. unicolor*, male emergence is more nearly synchronous in any given locality and is controlled by local climate.

Females. Close examination of the four *A. pacificus* broods indicate that the pattern of early postembryonic development is the same as in *A. unicolor*. Almost all of the shed chorions examined contained the embryonic cuticle, and very few of the spiderlings actually in the process of hatching had lost the chorion but not the embryonic cuticle. Therefore hatching involves the splitting and peeling back of the chorion and then the embryonic cuticle in close succession, followed by the (usually) simultaneous shedding of these membranes. The morphology of the embryonic cuticle and the first instar is as in *A. unicolor*.

The few data (Fig. 2) indicate that the timing of brood development of *A. pacificus* in nature may be similar to that of *A. unicolor*. Evidence that spiderlings may overwinter in the second instar and that adult females are long-lived was provided by an adult female (2246 at *R*) collected on 3 July. Although she was rearing no brood that year, her burrow was in the center of a 30 cm diameter aggregation of 36 burrows of spiderlings that matched the size and morphology of second instar *A. unicolor* spiderlings. Since she was isolated from other adult burrows, these spiderlings almost certainly belonged to her brood of the previous year. Data on brood size and egg size are given in Tables 3 and 4.

BEHAVIOR

Burrow structure. A. pacificus burrows (Figs. 16 and 17) are very similar in structure to *A. unicolor* burrows. The tubular burrow is slightly widened just below the entrance and at the bottom end and is narrowed between. The silk lining is thickest in the upper end, is often nearly imperceptible in the lower portion of the burrow, and tends to be thicker in less stable or dryer soil. There is considerable variation in burrow length among adult spiders (Table 6). These burrows tend to be longer in dryer soil, but many other factors also affect burrow length. Penultimate male burrows average smaller than those of adult females. Adult female burrow pitch ranged from 0 to 35° with most burrows between 0° and 15°. No burrow sloped upward from the entrance.

Entrance structure. This species possesses at its burrow entrance a flexible silken collar identical to that of *A. unicolor* (Figs. 18, 19, and 44). The only burrows observed with the collar closed and sealed on the inner surface with a small amount of silk (as is fairly common in *A. unicolor*) were those of three penultimate males apparently ready to undergo the final molt. Two burrows were found with soil plugs. In one burrow (2994 at Catherine Creek State Park, Ore.), the plug was in the entrance under the closed collar, but in the other (2970 at *V*), the plug was positioned one-third of the way down the burrow.

Egg sac structure and placement. All

four egg sacs examined were like those of *A. unicolor* (Fig. 16). Of the three egg sacs which I excavated, one (2825 at *S*) was near the top of the burrow, and the other two (at *I*) were in the bottom half (Table 6). All were attached to the ventral sector of the burrow wall.

Molting behavior. Fragmented exuviae were often found compacted like prey exoskeletons into the bottom end of burrows. Only two recently molted spiders were observed; two mature males each had the final exuvia packed lightly into the bottom end of its burrow. The exuvia of one male (2628 at *V*) was slightly broken, and the nature of the entrance closure could not be determined. The exuvia of the other (L-1 at *I*) was unbroken, and the collar was closed and lightly sealed inside with silk.

Defensive behavior. The behavior of foraging individuals of *A. pacificus* when disturbed by strong light and substrate vibrations is like that of *A. unicolor.* Adult females, when prodded, often assume an aggressive defensive posture like that of *A. unicolor.* Five large immature spiders at *R* were observed at the bottom end of their burrows spinning a thin septum of silk across the burrow lumen between themselves and the entrance as I excavated their burrows. When I broke the septa and prodded them, they exhibited the typical aggressive defensive posture.

Predators and parasites. Three recently digested males were found hanging in the webs of theridiid spiders at *G.* One male from Washington was taken "from the stomach of *Bufo boreus,*" a western toad. Three large immature specimens (2249 and 2640 at *R*, and 2114 at *M*) each had large nematode worms filling their abdomens. A pompilid wasp larva was found on the abdominal dorsum of a female *A. pacificus* on 26 July near Friday Harbor, Washington.

Prey capture behavior. Adult females were observed in foraging position within their open burrow entrances only after nightfall, or, rarely, in very dim light; the burrow entrances are normally closed during the daytime. Immatures usually assumed foraging postures earlier in the evening. Very young spiders frequently had collars open during the daytime and were often in foraging postures then. The foraging posture of this species is similar to that of *A. unicolor.*

Prey composition. Recently captured prey and identifiable prey rejectamenta found in the bottom of burrows include ants, beetles, spiders, hymenoptera (one vespid wasp and one Argidae), and Hemiptera. Ant and beetle remains were far more abundant than those of other groups. A 15-mm long carabid beetle (Broscinae) and *Camponotus* major worker ants were the largest prey found.

Disposal of prey remains. Fragmented exoskeletons of digested prey were frequently found mixed with a small amount of silk and packed into the bottom end of burrows as in *A. unicolor.* The thicker the cuticle, the less fragmented the remains. Live collembola were observed on such trash in a few burrows.

Mating behavior. Males of *A. pacificus* apparently wander in search of mates only at night. I have observed 12 wandering males, seven at *L* and five at *K*, all after nightfall. Considerable daytime collecting at both localities failed to turn up wandering males. Four male specimens from *W* are accompanied by the label "on ground at night." Wandering males usually stop moving when light is shown on them.

At *L*, two captured males were released near female burrows, and each stopped suddenly when it came close to a burrow. In one encounter, the female closed her collar just as it was discovered by the male, which then used his pedipalps and first legs in an apparent attempt to open the collar. After about 30 seconds it wandered away. In the second encounter, a female lunged out of her entrance toward the other male, made contact with its front legs, and both remained motionless for a few seconds. Then the female retreated quickly into her burrow and closed the collar. The male moved to the entrance, briefly handled the collar with its pedipalps and first legs, and then wandered away. Because of the handling of the males and the dim light used for observation, both encounters were probably abnormal. At *I*, the discovery of the first leg of a male *A. pacificus* on the soil surface at the burrow entrance of adult female 2232 suggested a male-female struggle. No male remains were found within this burrow.

Antrodiaetus occultus new species

ECOLOGY

Geographic distribution, elevation range, and habitat. This species appears to be limited to the relatively dry and warm valleys of the Willamette and Umpqua Rivers of western Oregon (Map 2). 0–600 ft (0–180 m).

LIFE HISTORY

Males. Adult males of this species apparently wander and mate during late September and October (Fig. 1). The data in Figure 3 indicate that there may be a partial temporal separation of the mating season of *A. occultus* from that of sympatric populations of *A. pugnax* and *A. pacificus*.

Antrodiaetus pugnax (Chamberlin)

ECOLOGY

Geographic distribution and elevation range. Northern Oregon, southern Washington, and northwestern Idaho (Map 2). 0–3500 ft (0–1100 m).

Habitat. I have observed *A. pugnax* at only two localities. At *B* on 8 July, a large population was located in a deciduous woods with a dense understory of shrubs and herbs along a small, flowing stream. Surrounding the woods was nonforested land, chiefly farmland. Although burrows were scattered throughout the woods on both horizontal and inclined ground, dense aggregations were found only beneath the densest vegetation. The soil was hard-packed brown loam with a high organic content, and was dry at the surface but slightly humid below 10-cm depth. The densest aggregation was found under the shelter of a large shrub on horizontal ground covered with scattered leaf and twig litter. Ten adult females, five penultimate males, and about 150 immatures were present in a 1-m^2 area. The habitat at Lewis and Clark Trail State Park, Washington (Fig. 64)—a dense deciduous riparian woods located at the bend of a river and surrounded by wheat fields—was very similar to the above habitat. The understory vegetation was dense, and the burrows were found in the more sheltered spots on both horizontal and sloping ground. The soil was firmly packed light brown silty loam with a slightly greater moisture content than at *B*.

Most of the other locality records for *A. pugnax* are in dry regions at low elevations near rivers or streams and therefore presumably in riparian woods similar to those described above. The only wooded habitats in the immediate vicinity of *C* are such riparian woods. *H* has similar habitats. However, one collection of *A. pugnax* at *E* was made in Douglas fir forest, a more humid habitat. Thus it appears that *A. pugnax* is chiefly found in the low elevation riparian deciduous woodlands of the dry interior portions of Washington and Oregon, and in the low, relatively dry forest of the valleys between the Coast Range mountains and the Cascade Range mountains.

LIFE HISTORY

Males. Collection data (Fig. 1) indicate that male wandering and mating occur within the period from late July to October.

Females. The limited data (Fig. 2) indicate that the timing of brood development in *A. pugnax* may be similar to that in *A. unicolor.* All individuals from which the brood size (Table 3) and egg size (Table 4) data were obtained are from *B* and Lewis and Clark Trail State Park, Washington. The second instar morphology is like that of *A. unicolor.*

BEHAVIOR

Burrow structure. (All observations on burrow and entrance structure and egg sacs were made at *B* and Lewis and Clark Trail St. Pk.) The burrow structure is similar to that of *A. unicolor.* The burrow is roughly tubular and slightly widened just below the entrance and at the bottom end (Fig. 20). The entire burrow is silk-lined, with the thickest lining in the upper portion. The lining is thicker in burrows with egg sacs, at least in the vicinity of the sac. Burrows vary considerably in size but are usually relatively small (Table 6). The longer burrows were in softer soil. All burrows but one were in horizontal ground; all these were vertical except for a slight turn at the bottom end of some. The burrow pitch of the burrow on sloping ground was 10°. The five penultimate male burrows observed averaged considerably smaller than the female burrows, were completely and rather heavily lined with silk, and had 0–5° burrow pitches. No burrows sloped upward from the entrance.

Entrance structure. Small immature spiders have flexible collar entrances similar to those of *A. unicolor.* The silk lining of the burrow is extended above the soil surface, stands erect when open, and collapses inward to close off and camouflage the entrance. Soil particles and ground litter fragments are incorporated into this collar. The burrow entrances of older spiders were sealed and plugged with soil (Fig. 20), making it difficult to determine the exact nature of the unsealed entrance. The closure varied from a thin septum of soil and silk only a few millimeters thick to a hard plug up to 15 mm thick, mainly of soil. Such a sealed entrance is very difficult to discover visually. The inside surface of the closure is covered with a lining of silk continuous with the burrow lining.

Egg sac structure and position. The egg sac structure of this species is very similar to that of *A. unicolor* (Fig. 20). The egg masses varied from 7 to 9 mm maximum diameter and 4 to 6 mm in thickness. Six of the eight egg sacs were positioned on the ventral sector of the burrow wall, the other two on lateral sectors. The egg sac silk appears to have the same texture and whiteness as burrow lining silk. All egg sacs but one were positioned just above the bottom end of the burrow (Table 6).

Behavior of brooding females. Like the large immature and nonbrooding adult spiders, all females with egg sacs had plugged and sealed entrances.

Predators. A female specimen collected at *G* on 15 April is accompanied by a label saying that she was the "prey of *Dinocnemis,*" a pompilid wasp.

Feeding behavior. Many young immature spiders were in foraging postures within their open burrow entrances during daylight, although more exhibited such behavior at night. Fragmented prey exoskeletons held together with small amounts of silk were found packed into the bottom ends of several burrows. Such rejectamenta from the burrow of a brooding female at *B* contained parts of two beetles.

Mating behavior. A label accompanying a male from *B* reports that the male was wandering over the ground surface at night.

Antrodiaetus montanus (Chamberlin)

ECOLOGY

Geographic distribution and elevation range. Primarily the Great Basin region from Utah and Nevada north to Washington (Map 2). 2500–7200 ft (750–2200 m).

Habitat. I have observed *A. montanus* in two localities. Near Pocatello, Idaho, on 26 July, a small aggregation of burrows was located in the bank of a dry ravine in juniper-sagebrush habitat at 4500 ft (Fig. 65). Burrows of three adult females and several immatures were found in an uneroded portion of the bank under a large juniper. The soil surface was covered with a thin layer of pieces of dead grass and juniper. The soil was extremely dry hard-packed loam down to 25 cm and dry looser gravel and loam below that. The bottom ends of the large burrows were about level with the ravine bed. At Crater Lake, Oregon, on 30 July, I observed a sparse population of *A. montanus* in open and dry lodgepole pine, fir, and spruce forest at 6000 ft. The two burrows observed were in rather unsheltered spots, one on horizontal ground. The soil was composed of volcanic "sand," very dry and loose at the surface, becoming firm at 5 to 10-cm depth and slightly humid below 15 cm. Scattered burrows of *A. pacificus* and *Atypoides gertschi* were also found at this locality.

The locality records in the Salt Lake City, Utah, area indicate that *A. montanus* is there found in dry, non- or sparsely wooded habitats along the lower portions of canyons and in the foothills of the mountains. All other locality records for this species are likewise from relatively xeric habitats similar to those described above.

LIFE HISTORY

Males. Collection data (Fig. 1) indicate that male wandering and mating occur within the period from early August through early November. Chamberlin and Ivie (1935, 1945) observed males wandering "in the autumn."

Females. Very limited data for *A. montanus* (Fig. 2) indicate that the timing of brood development may be similar to that of *A. unicolor.* The brood size and egg diameter of the single known brood of *A. montanus* (2160 at Pocatello) are given in Tables 3 and 4.

BEHAVIOR

Burrow structure. (Based on observations of three adult female burrows from Pocatello and one large immature female burrow from Crater Lake.) Burrow structure is quite similar to that of *A. unicolor*, except for a considerably greater average length (Fig. 21, Table 6). Two of the burrows were completely silk lined with the thickest lining in the upper part of the burrow. In the other two burrows, the lining below the upper 5 cm was barely perceptible. Burrow pitch ranged from 5 to 25°, and all burrows sloped downward. Chamberlin and Ivie (1933), who found a female *A. montanus* without a distinct burrow and under a cottonwood log, later (1935) erroneously stated that females of *A. montanus* "ordinarily do not have burrows." Their observation in a later paper (1945) was more accurate: "The female lives in burrows which extend about a foot or more straight down into the soil. The upper part of the burrow is lined with silk; the bottom is slightly enlarged, but not bent."

Entrance structure. (Based on observations of two adult female burrow entrances at Pocatello and one large immature female entrance at Crater Lake.) *A. montanus* constructs a flexible silken collar like that of *A. unicolor.*

Egg sac structure and position. The structure and means of attachment to the burrow wall of the single egg sac observed (2160 at Pocatello) were like those of *A. unicolor* egg sacs. Egg mass dimensions were 14 × 10 × 7 mm. The sac was positioned on the ventral sector of the burrow wall deep in the burrow (Fig. 21, Table 6). Chamberlin and Ivie (1945) also found egg sacs only in the lower portion of the burrow.

Behavior of brooding females. When collected in the evening before dark, the single brooding female (2160 at Pocatello) had a closed but unsealed collar.

Parasites. The abdomen of a large immature *A. montanus* (0174) from Steens

Mountain, Oregon, was filled with a nematode worm.

Feeding behavior. The two large immature *A. montanus* females from Crater Lake were collected after dark in foraging positions just inside their open collars. Fragmented prey exoskeleton was found mixed with silk and packed into the bottom ends of the burrows of all three adult females from Pocatello. Two of these trash packets contained the remains of 12 medium to large-sized beetles.

Mating behavior. Apparently *A. montanus* males wander in search of mates at night and remain under the shelter of various objects during the day. One male from Verdi, Nevada, was collected walking over the ground at night. Chamberlin and Ivie (1945) often collected adult males "under stones, sticks, [and] bunches of grass" presumably during daylight hours. A label with the holotype male notes that it was resting under a piece of sagebrush.

Antrodiaetus hageni (Chamberlin)

ECOLOGY

Geographic distribution and elevation range. South-central British Columbia, eastern Washington, and eastern Oregon (Map 2). 1000–4000 ft (300–1200 m).

Habitat. I have observed *A. hageni* at only one locality—at Trail, British Columbia, on 13 July on the slopes along a dry stream bed in a large nonforested ravine one mile from its junction with the Columbia River (Fig. 66). The vegetation consisted of scattered young poplar trees and large deciduous shrubs. Much of the soil surface was without plant or litter cover. The soil was chiefly deep sand with a few rocks and very little organic material. The upper 3–8 cm of the sand was hot, dry, and loose; below that it was humid, well packed, and much cooler. Burrows were found in both steeply inclined and horizontal ground, but were usually clustered in more sheltered spots where the soil surface was stable, such as under trees and shrubs. *A. hageni* was not found in the cooler, humid forest habitats near Trail.

Near Baker, Oregon, where *A. hageni* has been collected, I unfortunately searched only in humid forest habitats and there found only *A. pacificus*, evidence that *A. hageni* is here found in the drier habitats (with sparser vegetation) at and below 4000 feet. An adult female *A. hageni* from near Oliver, British Columbia, was collected on a dry "sandy-rocky slope" covered with bunch grass and sagebrush (E. Thorn, personal communication). All other British Columbia records of *A. hageni* are in low river valleys where dry habitats similar to this and to that along the Columbia River at Trail are common; it is probably safe to assume that the habitat at Trail is an approximately normal *A. hageni* habitat.

LIFE HISTORY

Males. Adult male wandering and mating apparently occur within the period from late July through October (Fig. 1).

Females. Two records (Fig. 2) weakly indicate that the timing of brood development is similar to that of *A. unicolor*.

BEHAVIOR

Burrow structure. (Based on observations of two adult female and two immature female burrows.) The burrow architecture (Fig. 22, Table 6) is similar to that of *A. unicolor*. The roughly tubular burrow is somewhat enlarged just below the entrance and at the bottom end. All burrows were entirely silk lined, with the lining of the collar and upper part of the burrow much thicker than the rest of the lining. The two penultimate male burrows observed were similar to the female burrows in structure. Burrow pitch ranged from 0 to 35°, and all sloped downward.

Entrance structure. (Based on observations of one adult female and two large immature female burrow entrances.) *A. hageni* constructs a flexible silken collar very similar to that of *A. unicolor* (Figs. 45–46).

Molting behavior. An immature spider which molted within a glass tube in captivity fragmented its shed exuvia several days after ecdysis.

Predators. A large immature female of *A. hageni* was collected together with a pompilid wasp, *Priocnemis oregona* Banks (identification, H. E. Evans), on 7 April at Baker, Oregon. Unfortunately, no other data was included with the specimens. It is probable, however, that *A. hageni* is a host of this wasp, since the three other host species records for this wasp are mygalomorph spiders, one being *Atypoides riversi* (Wasbauer and Powell, 1962).

Feeding behavior. All burrow entrances were closed during the afternoon of observation. Prey remains were found packed into the bottom end of the burrow of one large immature female. The prey exoskeletons were fragmented (the thinner the cuticle the smaller the fragments) and held together with a small amount of silk. Identifiable prey consisted of 12 ants, two beetles, one dipteran, and two adult male spiders (*Tegeneria domestica* and *Xysticus* sp.).

Antrodiaetus cerberus new species

ECOLOGY

Geographic distribution, elevation, and habitat. Known only from the type locality in coniferous forest in northeastern Washington. Approximately 2000–2500 ft (600–750 m).

LIFE HISTORY

Males. All four examined males of this species were collected in pitfall traps sometime during May, 1962 (Fig. 1). Three more males were collected sometime during April and May, 1962 (W. Ivie, personal communication). It is thus likely that *A. cerberus* males wander and mate only during the spring.

Females. Two records (Fig. 2) weakly indicate that brood development timing may be similar to that of *A. unicolor.*

Antrodiaetus yesoensis (Uyemura)

ECOLOGY

Geographic distribution and habitat. Known only from the northern Japanese island of Hokkaido, where it is presumably found in the conifer forest of that cool temperate climate (Map 3).

LIFE HISTORY

Males. The few records (Fig. 1) indicate that the period of male wandering and mating occurs during the summer months.

Antrodiaetus lincolnianus (Worley)

ECOLOGY

Geographic distribution and elevation range. Eastern Kansas and eastern Nebraska (Map 1). 700–1200 ft (210–360 m).

Habitat. In 1928, Worley stated that the holotype male and the three paratype males were collected "on clay banks near deciduous forest" at Lincoln, Nebraska. Later (Worley and Pickwell, 1931), he stated that these males were found "under logs in woods" apparently in their own burrows. H. S. Fitch (personal communication) collected a wandering male near Lawrence, Kansas, about 35 m from a large patch of deciduous forest through which ran an intermittent stream with high banks. This limited evidence, in addition to the fact that no specimens of *A. lincolnianus* have been collected in localities removed from the western lobes of the eastern deciduous forest, indicates that this species is probably found in somewhat humid forest habitats.

LIFE HISTORY

Males. Male wandering and mating in *A. lincolnianus* apparently occur during late winter and early spring. The seven adult males indicated in Figure 1 were collected by four different collectors on seven different dates during four different years. Also, two other males, which I have been unable to examine but which are almost certainly *A. lincolnianus*, were collected by yet a different collector, Scheffer (1906), in Manhattan, Kansas, on 5 April during yet another year. Such a scattering of individual collecting events makes it more likely that these dates indicate the actual wandering and mating period of this species.

Females. The single gravid female record (Fig. 2) for *A. lincolnianus* hints that the timing of brood development may be similar to that of *A. unicolor.*

BEHAVIOR

Burrow structure. Worley and Pickwell (1931) state that "this species is very similar in habits to *B. pacificum* Simon [=*A. pacificus*] of the Pacific Coast, constructing burrows in the ground six to ten inches deep and lining them with silk."

Antrodiaetus stygius new species

ECOLOGY

Geographic distribution and elevation range. Missouri and northern Arkansas (Map 1). 400–1500 ft (120–460 m).

Habitat. I have observed *A. stygius* only at Bennett Springs State Park, Missouri, on 4 September. An aggregation of approximately 100 adult and immature burrows in a 4-m² area was found on a 20–35° slope 3–5 m from the edge of a large spring-fed stream in the heavy shade of a mixed deciduous forest (sycamore, elm, and oak trees common). The ground surface had a sparse to dense cover of leaf litter. The hard-packed dark brown loam soil was slightly humid at the surface and increasingly humid downward. A wandering adult male was collected near a stream near Warrensburg, Missouri, in a similar deciduous forest of oak, sycamore, and elm (Peck, 1966).

LIFE HISTORY

Males. The limited data (Fig. 1) indicate that adult males wander and mate during the fall.

Females. All three broods observed had developed beyond the hatching stage, but every shed chorion contained the embryonic cuticle, an indication that the pattern of early postembryonic development is similar to that in *A. unicolor.* Also the morphology of the embryonic cuticle, the first instar, and the second instar is very similar to that of *A. unicolor.* The limited data (Fig. 2) indicate that the timing of *A. stygius* brood development in nature resembles that of *A. unicolor.* The size of the only complete brood is given in Table 3.

BEHAVIOR

Burrow structure. The three brooding female burrows observed were completely silk-lined and shaped much like *A. unicolor* burrows: roughly tubular and slightly widened just below the entrance and at the bottom end (Fig. 23, Table 6). Three penultimate male burrows were shaped similarly but had thinner silk linings and were shorter (Table 6). All six of these burrows were slightly sinuous and nearly vertical, with burrow pitches of 15–30°.

Entrance structure. All burrows discovered—even those of immatures—had their entrances sealed over and usually plugged with soil (Fig. 23), making it difficult to determine the exact nature of an unsealed entrance, which appeared to consist of a flexible collar. The upper 4–10 mm of the larger burrows was packed with soil. The bottom of this plug was lined with silk continuous with the burrow lining, and the upper exposed surface closely matched the surrounding soil surface in texture and color.

Egg sac structure and position. The shape and structure of the two *A. stygius* egg sacs observed appeared similar to those of *A. unicolor.* Both were positioned on the ventral sector of the wall in the bottom half of the burrow (Table 6). The burrow diameter at the region of egg sac attachment may have been greater than normal, but the sacs still produced a slight localized construction of the burrow lumen. The silk lining was thicker in the vicinity of the egg sac than elsewhere below the upper end of the burrow. Egg sac silk appears to have the same texture and white color as burrow lining silk.

Behavior of brooding females and broods. The burrow entrances of brooding females, like those of nearly all other individuals, were sealed with soil plugs. The brood composed of first instar spiderlings was still enclosed within the egg sac, while both second instar broods were entirely outside the sac. In one of these latter two broods, the egg sac was no longer present; in the other it contained all the first instar exuviae, indicating that the spiderlings emerged from the egg sac after molting into the second instar. The second instar spiderlings were quite active.

Defensive behavior. Some adult females assumed a defensive posture in the bottom of their burrows similar to that of *A. unicolor.*

Predators. A pompilid wasp cocoon containing a larva was found in one medium-sized *A. stygius* burrow. Small pieces of spider exoskeleton were attached to the outside of the cocoon.

Disposal of prey remains. Fragments of prey cuticle were found packed into the bottom end of one adult female burrow.

Antrodiaetus apachecus new species

ECOLOGY

Geographic distribution and elevation range. Mountains of Arizona and New Mexico (Map 4). 6100–8500 ft (1850–2600 m).

Habitat. I have collected *A. apachecus* at only one locality, near La Cueva, New Mexico, at 7800 ft in a somewhat open forest of yellow pine, spruce, and fir. An aggregation of six burrows was found under the overhang of a large rock on the slope of a wide ravine. Aspen and scrub oak were common in the ravine. The ground surface under the rock lacked leaf litter, and the soil was humid dark sandy loam with some pebbles. All other locality records for this species are either from transition zone forest or low Canadian zone forest. Because it is restricted to such high elevation habitats, the species population is presently fragmented into several geographically isolated populations each on a forested montane "island" surrounded by unfavorable nonforested habitats at lower elevations.

LIFE HISTORY

Males. Collection data (Fig. 1) indicate that male wandering and mating occur from midsummer to early fall.

BEHAVIOR

Burrow structure. The burrows of only four medium- to large-sized immature spiders were observed. The burrow shape appeared similar to that of *A. stygius*, i.e., tubular but slightly widened just below the entrance and at the bottom end. The silk lining was very thin and possibly absent over most of the burrow, but slightly thickened at the upper end. The burrows were slightly sinuous and nearly vertical, with a burrow pitch of 10–20°.

Entrance structure. The burrow entrance of only one immature spider was observed and appeared to consist of a short thin flexible collar.

Feeding behavior. A medium-sized immature *A. apachecus* was found at the bottom of its burrow feeding upon a dead, partly digested, 20-mm long lepidoptera larva covered with urticating setae. This was at 11:00 A.M. and the collar was closed.

Antrodiaetus roretzi (L. Koch)

ECOLOGY

Geographic distribution. Central portion of the Japanese island of Honshu (Map 3).

Habitat. According to Yaginuma (1962), *A. roretzi* is usually found in humid, often heavily shaded habitats. Yamamoto (1942) found a sizeable burrow aggregation scattered over a very steep bank composed of reddish soil. Bamboo was growing over the upper part of the bank. Komatsu (1942) reported that this species is found in shaded humid habitats, often on inclines or banks. Uyemura (1936) found a burrow on a steep slope in moss-covered soil at the base of a pine tree. Ohe (1966) found burrows chiefly on inclines (40–90°) of banks along a trail. Such burrows were frequently in the shelter of exposed tree roots near the top edge of these banks or were under the overhang of exposed rocks. All but a few burrows were located on the upper two-thirds of such banks. He found burrows both in heavily shaded moss-covered portions of banks and in less well-shaded spots where the surface soil was rather dry. Burrows are also often found in caves (Yaginuma, 1962; Komatsu, 1961) near the entrances. Komatsu (1942) found an aggregation of over 100 burrows on an inclined surface in humid reddish soil in dim light just inside the entrance of one cave.

LIFE HISTORY

Males. The small amount of data in Figure 1 indicates that male wandering and mating may occur during winter and early spring. More data are needed.

Females. Ohe (1966) observed spiderlings in parent burrows "from September on."

BEHAVIOR

Burrow structure. Yamamoto (1942) observed the burrows of two adult males and several adult females (Table 6). These were tubular and silk lined. Burrows in soft soil free of obstacles were longer than those in harder soil with roots, and male burrows averaged shorter than adult female burrows. The burrow pitch of the two male burrows was apparently about 0–10°. Komatsu (1942) observed several vertical burrows in inclined ground, but most were roughly perpendicular to the soil surface. Ohe (1966) described and illustrated the variation observed in the inclination, shape, and length of a large number of *A. roretzi* burrows (probably both adult and immature). Most burrows apparently were not strongly curved and were roughly perpendicular to the plane of the adjacent ground surface. Exceptions were the result of root or rock obstacles. Most burrows were approximately 20 cm long or shorter, but a few reached 30 cm.

Entrance structure. A pair of photos of an *A. roretzi* burrow entrance has been published twice (Komatsu, 1937 and 1961). Drawings of the entrance can be found in Komatsu (1961), Yamamoto (1942), Yaginuma (1960), and Ohe (1966). Descriptions, all very brief, are found in Yamamoto (1942), Komatsu (1942), Yaginuma (1962), and Ohe (1966). All these describe the structure as a "double door entrance." After studying the fine photos and drawing of Komatsu, it appears to me as though the double door nature of the entrance has been overemphasized and that the entrance structure is more accurately described as a collapsible collar which is reduced at two opposing portions, leaving two lateral flaplike sectors that operate roughly as separate doors. Such a structure is quite similar to that of the collars of some adult *A. unicolor* burrows. Clearly, additional careful field observations are required. Komatsu (1942) and Ohe (1966) observed that, in entrances on an inclined ground surface, the collar is reduced at its ventral and dorsal sectors with both lateral flaps "hinging" on opposing dorsoventral axes. Such an orientation is common in *A. unicolor.* The collar in Komatsu's photos is constructed of silk and soil, well camouflaged exteriorly, and silk lined on the inner surface, this silk lining apparently being continuous with the burrow lining. Ohe found that collars in moss-covered soil were constructed partly of moss and were difficult to discover. Although Ohe (1966) observed a few burrow entrance openings as large as 1.5-cm diameter, most were roughly 1 cm in diameter.

Molting behavior. Yamamoto (1942) collected two adult males in their own burrows. In one, the shed exuvia lay on the ventral sector of the burrow wall about one-third of the way down the burrow, and a maze of silk threads occupied much of the lower half of the burrow, with the male in the bottom end. The second male had spun a thin silk septum across the inside of the entrance, and no exuvia or silk thread mazes could be found in the burrow. Yamamoto did not say whether either collar was closed or open. Possibly the second spider had sealed the inside of the collar shut. Clearly, additional observations are needed to clarify behavior during the final male molt of *A. roretzi.*

Atypoides riversi O. P.-Cambridge

ECOLOGY

Geographic distribution and elevation range. A coastal population in northern California west of the Central Valley as far south as the Monterey Peninsula, and a Sierran population in the Sierra Nevada Mountains and their foothills (Coyle, 1968). These populations are probably geographically isolated. 200–1800 ft (60–550 m) (coastal population). 2000–8000 ft (600–2400 m) (Sierran population).

Habitat. Coastal population: Rivers (1891; O. P.-Cambridge, 1883) found *A. riversi* burrows in both pine and deciduous forests, often in stream banks. Smith (1908) found burrows "abundant along shaded streams and in thickets in the foothills and mountains" of the Coast Range. Gertsch's (1949) habitat description was similar. I have collected coastal *A. riversi* in three localities, and will summarize my observations below.

A. riversi is found in the foothills and mountains of the Coast Range, chiefly in shaded forest habitats. These may be deciduous, pine, or mixed deciduous-pine forests. Interestingly, *A. riversi* is uncommon or absent from the famous "basin forest" of predominately coast redwood and Douglas fir; I searched hard in such habitats at three localities unsuccessfully. *A. riversi* burrows are common in the next highest vegetation zone, the tan oak-pacific madrone forest containing only scattered coast redwood trees (Fig. 67). Burrows are found chiefly on rather steep inclines of banks along trails, roads, and streams. The surface litter in these spots ranges from absent to quite thick. The soil varies from compact sandy loam to clay loam, sometimes with a high pebble content. These soils are usually dry at the surface during the summer, but below about 10-cm depth are at least slightly humid. The densest burrow aggregations are found on stable, noneroding banks. Three adult females and 29 immatures were found in a 0.30-m^2 area at *C.*

Sierran population. I have observed *A. riversi* in three different locations above 6500 ft in the Sierra Nevada Mountains. The habitat ranged from open pine-fir forest to dense pine-fir or California red fir forest. The densest and largest population was found in the red fir forest at *G.* Burrows are found on both steeply sloping stream and road banks and on gently inclined ground. The surface litter varied from absent to very thick. The soil was brown sandy loam, dry and loose at the surface but becoming humid and packed at from 3 to 15 cm deep. The lower the rock content of the soil, the greater is the burrow density.

LIFE HISTORY

Males. Coastal populations: Male wandering and mating in these populations may not normally begin until September, October, or November (Fig. 1), and may coincide with the onset of the fall and winter wet season. At *D* and *F* on 14 and 15 August, I searched both day and night in areas of dense burrow concentrations for adult males but found none. *Sierran populations*: In at least the higher populations

(6500–8000 ft), male wandering and mating commence earlier and probably (because of harsh winter weather) terminate earlier (Fig. 1).

There is some evidence to indicate that the palpal tarsi of immature males of *A. riversi* may be swollen during more than just the penultimate instar and that many of the immature males with swollen palpal tarsi found in late summer or fall may not mature until one year later. The shed exuvia of an immature male collected at *H* on 8 August had swollen palpal tarsi like those of the newly formed instar. The exuvia of a recently molted immature male collected at the same locality and time had unswollen palpal tarsi, whereas those of the new instar were swollen. Thirteen actively foraging immature males with swollen palpal tarsi were collected at *G*, *H*, and *I* from 6 to 9 August when adult males were wandering. At *D* and *F* on 14–15 August, 14 immature males with swollen palpal tarsi were trapped in foraging postures in their burrow entrances at night, and seven were dug out of closed and usually (five) sealed burrows. All 21 were kept cool and humid in an ice chest, but only the latter seven molted to maturity.

Females. Coastal populations: The pattern of early postembryonic development of *A. riversi* appears to be similar to that of *Antrodiaetus unicolor.* All of the many shed chorions observed in each of the six egg sacs with first instar spiderlings have the embryonic cuticle attached, indicating that both the chorion and embryonic cuticle split and peel off simultaneously or in close succession and are then shed together. The morphology of the embryonic cuticle, the first instar, and of the second instar of *A. riversi*, is also quite similar to that of *A. unicolor*, with the obvious exception that the anterior lateral spinnerets are not lost in the second instar of *A. riversi*. The data on the timing of brood development in *A. riversi* (Fig. 2) indicate that eggs are laid in summer, that brood development reaches the second instar by mid-autumn, and that the spiderlings abandon the parental burrow before the following summer. Rivers (1891) observes without further comment that "there is a period of aestivation, but the cause is not yet investigated." Data on brood size and egg size are given in Tables 3 and 4. *Sierran populations:* Only a single Sierran brood was collected (at *I*). Its size and egg size are given in Tables 3 and 4.

Behavior

Burrow structure. A. riversi has a roughly tubular silk-lined burrow which normally increases slightly in diameter from the top to near the bottom end where there is usually a decrease in diameter so that the last 2–4 cm are narrow (Figs. 24 and 25). In the Sierran populations, this terminal constriction was less noticeable at *H* and *I* but was well developed at *G*. The white silk lining is usually quite thick in the turret and upper part of the burrow, becoming thinner in the bottom portion, and may be nearly imperceptible for the last few centimeters. Burrows with egg sacs usually had thicker silk linings than those without. Burrow dimensions, which show considerable variation, are given in Table 6. As might be expected, larger individuals within a population have larger burrows, and this correlation is shown in the lower mean burrow dimensions of the Sierran populations, which have, on the average, smaller mature individuals than the coastal populations. Also, penultimate male burrows average smaller than adult female burrows. Burrows ranged from vertical to near horizontal, but the burrow pitch ranged within 0–15°. Rivers (1891) also observed that the burrows "were more or less perpendicular" to the ground surface.

The descriptions of coastal *A. riversi* burrow structure by Rivers (1891), Smith (1908), and Gertsch (1949) are in agreement with my observations, except for the statement by Rivers that an adult female burrow "is more roomy at the base than at the opening." He apparently overlooked the terminal constricted portion. Smith, like myself, observed that "the tunnels are commonly considerably reduced in diameter for the last two centimeters. . . ."

Entrance structure. The silk lining of the burrow is extended above the soil surface to form a rather rigid elongate collar or turret (Figs. 26, 47–50), hence the common names "Californian turret builder" (Rivers, 1891) and "the turret spider" (Gertsch, 1949). This turret is smooth white silk on its inner surface and is camouflaged and kept erect by attached soil particles and usually also organic materials (from the ground surface litter) such as pieces of twigs, leaves, needles, bark, and moss. Normally the turret wall is supported at its base by the thickest accumulation of soil and other materials and becomes thinner distally. The opening at the top of the turret is roughly circular, and the rim is slightly expanded to form a lip. The entrance is closed off by collapsing or folding in only the distal end of the turret. Sometimes, as when a spider is molting, this closure is sealed on the inside with a small amount of silk.

There is considerable intrapopulation variation in turret height, as well as a marked tendency for individuals of the Sierran populations to have shorter turrets than those of the coastal populations (Table 6). A possible reason for this difference (other than geographic variation in genetically determined turret building behavior) is that snow accumulation may annually destroy the Sierran turrets, whereas coastal turrets are probably accumulations of several years' additions. A few turrets in the Sierran populations incorporated needles, twigs, or leaves consistently attached by their ends and radiating out roughly horizontally from the turret (Fig. 50). This radial arrangement closely resembles the "twig-lining" arrangement found in some of the Australian aganippine trapdoor spiders (Main, 1957a), but at present there is no evidence that in *A. riversi* it has a similar functional significance in prey detection.

The descriptions of coastal *A. riversi* turret structure by O. P.-Cambridge (1883), Rivers (1891), Smith (1908), and Gertsch (1949) are in agreement with my observations. Both Rivers and Smith describe considerable variation in the litter material used in turret construction. Smith includes two photographs illustrating some of this variation. Rivers observed turrets as tall as 3 inches (= 7.6 cm).

Egg sac structure and position. The egg sac structure (Fig. 24) and egg mass shape of *A. riversi* is very similar to that of *Antrodiaetus unicolor*. Mean dimensions for the three egg masses are 10 × 9 × 6 mm. Egg sac silk appears to have the same texture and whiteness as burrow lining silk. In each of the nine burrows with egg sacs, the sac was positioned about half way down the burrow (Table 6). In five burrows the egg sac was on the ventral sector of the burrow wall, in three on the dorsal sector, and in one on a lateral sector. Some burrows may have been widened somewhat in the region of egg sac placement, but each sac produced a localized constriction of the burrow lumen.

Behavior of brooding females and broods. All of the first instar broods were completely enclosed within egg sacs, but the thickness of the silk of three of these egg sacs had been much reduced and the spiderlings could be seen moving around very slowly within. It would be interesting to know whether these spiderlings (or the parent) possibly possess silk-digesting enzymes. All nine burrows with egg sacs had open turrets. Three of these were found at night, each with the female in foraging position in the top of the turret. It therefore appears that brooding females remain active at least until the spiderlings emerge from the egg sac.

Molting behavior. Molting behavior in *A. riversi* appears similar to that of *A. unicolor*. Four recently molted immature spiders were collected during the second week of August. In each case the top of the turret was closed and the edges held together by a thin layer of silk spun over the inside of the closure. The recently shed exuvia was attached to the ventral sector of the burrow wall two-thirds to three-fourths of the way down the burrow, venter against the wall, anterior end heading up the burrow, and with legs and pedipalps extended on the wall. The unsclerotized spiders were in the very bottom end of the burrows. Five penultimate males (from *D* and *F*) that later molted in captivity and several other immature males with swollen palpal tarsi were collected at other localities in similarly closed and sealed burrows. A fully sclerotized adult male ready to emerge was collected at *I* in a sealed burrow with the last exuvia packed into the bottom end of the burrow.

Defensive behavior. When spiders in foraging positions were disturbed by light or substrate vibrations, they retreated rapidly down the burrow without closing the top of the turret. During the later stages of excavating to expose a burrow, one finds the spider backed up tightly into the narrowed bottom end of the burrow in a stereotyped defensive posture. The cephalothorax is tilted backwards at approximately a 45° angle with the abdomen and is therefore in contact with the sector of the burrow wall dorsal to the spider. Legs IV and III, and possibly II, hold onto the burrow wall to anchor the spider, and the other legs and pedipalps are spread apart laterally. The chelicerae are also elevated and spread apart laterally with fangs extended. If prodded, the spider strikes with a sudden downward movement of the cephalothorax and chelicerae. Penultimate males also exhibit this same behavior. Such a behavior pattern, like that of *A. unicolor,* obviously confines the approach of an attacker to that part of the spider protected by its chelicerae, but the narrowed burrow end of *A. riversi* probably provides more effective protection for its abdomen than the enlarged burrow ending of *A. unicolor.* Smith (1908) observed that the terminal constriction makes "a snug fit for the spider, and here it usually snuggles down tightly when the digging [of the collector] has reached the limit necessary to secure the specimen."

Predators. Wasbauer and Powell (1962) observed predation on *A. riversi* at Felton (Santa Cruz Co.), California, on 5 May, by the pompilid wasp *Priocnemis oregona* Banks. (See *Antrodiaetus hageni* predator records.)

Feeding behavior. The foraging posture of *A. riversi* appears similar to that of *A. unicolor;* the spider is within and facing up the turret with the pedipalps and legs I extending forward, touching the silk lining on or below the turret lip. No adult spider was ever found in this foraging position until the arrival of full darkness. Unlike other species of *Atypoides* and *Antrodiaetus,* most individuals of *A. riversi* were found to leave their turrets open both day and night.

A. riversi, like *A. unicolor,* apparently detects prey primarily, if not solely, through the substrate vibrations transmitted via the silk lining of the turret and burrow. I was able to elicit prey capture responses by gently vibrating with forceps the ends of turret litter. The needles, twigs, leaves, and other somewhat linear litter that are often incorporated into the turret of *A. riversi* probably extend the prey-sensing radius of the spider even when, as is usually the case, this litter is not arranged radially. However, it remains to be shown whether or not attaching linear litter to the turret is a result of selection for improved prey sensing.

Fragmented prey cuticle is often found packed into the bottom end of the burrow and sometimes in other parts of the burrow wall as well. A cursory examination of trash indicates that ants may make up a large part of the prey of this species. Identifiable portions of several *Camponotus* workers were found.

Smith (1908) briefly commented on the

feeding behavior of young immatures of *A. riversi* collected from coastal populations and kept in the laboratory. These accepted both small ants and aphids, and always maintained a hold on the lip of the turret with the claws of legs IV during the lunge for prey.

Courtship and mating behavior. There are no published observations of courtship or mating in the family Antrodiaetidae. I was fortunate enough to witness a portion of mating behavior between a pair of *A. riversi* at *G* on 8 August 1967, at 9:45 P.M., about 45 minutes after nightfall. When first discovered, the male was positioned within and just below the rim of the female's turret facing down into the burrow with the tarsi of legs IV on the turret rim (Fig. 27). The female was immediately below the male and facing up the burrow in a posture very similar to the normal defensive posture, except that her fangs were unextended. The male's cephalothorax was raised slightly and its cheliceral apophyses were positioned as a unit between the outspread chelicerae of the female (Fig. 28). It appeared as though the male was applying substantial pressure with his chelicerae, but the female did not struggle. I could not observe exactly how the pedipalps and legs I, II, and III of the male were positioned, but the pedipalps appeared to be extended beneath the female and legs III and probably legs II were holding onto the burrow wall below legs IV. After two minutes in this position the female struggled and was forced down the burrow by the male, which appeared to maintain his hold with his cheliceral apophyses. I am not certain that the pair was actually copulating when discovered.

Adult males apparently wander in search of mates only at night. Even though I searched during both daylight and evening hours, the Sierran males were found wandering on the ground only after 9:30 P.M., at least half an hour after nightfall, and the largest numbers were found between 10:30 P.M. and midnight, when the searching ended.

Atypoides gertschi Coyle

ECOLOGY

Geographic distribution and elevation range. Cascade Mountain Range and foothills from southern Oregon south and east into the northern end of the Sierra Nevada Mountains of California (Coyle, 1968). 2000–7500 ft (600–2300 m).

Habitat. The densest and largest populations of *A. gertschi* were found above 6000 ft in the open California red fir forest at *N* and *P* (Fig. 68). In this habitat, ground cover vegetation is nearly absent and the surface litter generally sparse. The soil is volcanic "sand" or sandy loam, dry and loose at the surface, but becoming humid and packed 5–15 cm below. Burrows were found both on level ground and inclined surfaces. At lower elevations burrows are often common in open forests with little ground vegetation or in nonforested areas of manzanita chaparral in volcanic "sand" soil, as long as the soil is humid below 5–15 cm. For instance, at *O* I found a dense population in manzanita chaparral only along the edge of the lake. The habitat at *M* is rather artificial because of the great variety of imported vegetation, but it is wooded and the soil is sandy. Most of the burrows there were along the side of a stream (W. J. Gertsch, personal communication).

LIFE HISTORY

Males. The collecting data in Figure 1 indicate that male wandering and mating occur during the summer.

Females. Only a single brood of *A. gertschi* (from *N*) has been collected (Fig. 2). The absence of broods with the many other females that I excavated is puzzling, but it is possible that brooding females of this species tend to keep their entrances closed nocturnally and were missed because of the difficulty of spotting closed entrances. Many females—all collected in late summer—contained small developing eggs that appeared to be timed for spring or summer oviposition. The morphology of the first instar is very similar to that of *A. riversi.* All of the shed chorions examined contained the embryonic cuticle, an indication that hatching is also similar to that in *A. riversi.* The size of the known brood is shown in Table 3.

BEHAVIOR

Burrow structure. (See Table 6 for burrow measurements.) The burrow is roughly tubular, with a slight expansion in diameter just below the entrance and a larger increase in diameter at the bottom end (Figs. 29–30). It is well lined with silk just below the entrance in the usually dry, loose surface soil, but the thickness of the lining decreases with depth as the soil increases in humidity and stability so that there is usually only a very thin lining over much of the rest of the burrow. The long axis of the upper portion of all burrows was nearly perpendicular to the plane of the adjacent ground surface. Almost every burrow curved to nearly horizontal at the bottom end.

Entrance structure. The tubular silk lining of the burrow extends above the ground surface to form a rather thick but flexible collar which is collapsed inward to close off the entrance (Figs. 31–34; 51–53). The collar is composed chiefly of soil particles and small bits of surface litter held together by silk so that a closed entrance is remarkably well camouflaged. When open, this collar normally does not remain erect, but collapses outwardly so that it is roughly parallel to the ground surface. Usually only the proximal portion of the inner surface of the collar is a clean white extension of the burrow lining. The burrow entrance opening is often slightly elliptical. As in *Antrodiaetus unicolor,* a closed collar usually gives the appearance of a "double door" (which it is not) because the spider collapses the collar in a bilateral manner by pulling inwardly on two opposing (lateral) sectors, producing a condensation of folding at the two opposing points where these sectors meet. The collar is often somewhat reduced at these two opposing points, which correspond to the ends of the long axis of an elliptical entrance opening. No sealed collars were found.

Egg sac structure and position. The only *A. gertschi* egg sac collected appeared to be very similar in size, shape, and construction to those of *A. riversi* (Fig. 29). It was attached to the ventral sector of the burrow wall less than one-third of the way down the burrow at a point where the burrow appeared to have been slightly enlarged, but the sac produced a localized constriction of the burrow lumen.

Molting behavior. A recently molted female spider (2016 at *M*) was collected on 31 July. The burrow entrance was closed but unsealed, and a plug of soil had been placed one-third of the way down the burrow. The weakly sclerotized spider was in the bottom of the burrow. The exuvia, heading up the burrow and with legs extended, was lightly attached to the silk lining of the ventral sector of the burrow wall several centimeters from the bottom end.

Defensive behavior. When a female in foraging position was disturbed by light or substrate vibration, she either rapidly withdrew down the burrow without closing the entrance or suddenly closed the collar with her pedipalps and anterior legs and held the collar shut without retreating.

Feeding behavior. Burrow entrances were closed during daylight hours. The youngest spiders opened their entrances and assumed a foraging posture earlier than older spiders, often as soon as it became twilight. Mature females usually opened their entrances well after nightfall. The foraging posture of *A. gertschi* appears similar to that of *A. riversi,* with pedipalps and anterior legs resting on the basal portion of the collar. If the plane of the burrow opening is not horizontal, the spider usually orients this stance with its venter against the lowest sector of the burrow opening, which is also usually the long end of an oval entrance opening. The exoskeletons of two freshly digested *Camponotus* worker ants were found in one adult female burrow, and ant pieces were observed on the ground surface next to another burrow. Only occasionally was prey cuticle found in burrows.

Courtship and mating behavior. Males of *A. gertschi* apparently wander only after dark. All wandering males (14) that I have collected were found after 10 P.M. even though collecting included both daylight hours and the period from 8 to 12 P.M. A female at *O* was discovered at 11 P.M. feeding on a recently killed conspecific male several centimeters below her burrow entrance.

Atypoides hadros Coyle

ECOLOGY

Geographic distribution and elevation range. Southern Illinois and eastern Missouri (Coyle, 1968). 400–1100 ft (120–330 m).

Habitat. I have observed *A. hadros* at only two localities. At Ferne Clyffe State Park, Illinois, burrow aggregations were found in shallow shelter caves cut into the base of steep limestone bluffs. Mixed hardwood forest extended along the base of these bluffs. Burrows were found only in those shelter caves kept moist by water seepage in late summer. The largest aggregation of burrows was found on the floor of the most humid shelter, where males, females, and immatures of both *A. hadros* and *Antrodiaetus unicolor* lived side by side. The soil was a moist to wet mixture of soft clay-loam and pebbles. Surface litter was absent. Burrows were present both at the well-lighted edges of the shelter caves and in the dimly lit areas. Except in the most humid shelter cave, *A. unicolor* was more abundant than *A. hadros.* At Montauk State Park, Missouri, burrows of both *A. hadros* and *Antrodiaetus* were found side by side in moist reddish clay-loam with very little surface litter at the base of a high rock outcrop on the bank of the Current River in mixed hardwood forest.

The other three localities where *A. hadros* has been collected (Little Grand Canyon, Pine Hills, and Lusk Creek, Illinois) are also in forested areas where ravines, rock outcrops, and other sheltered spots are common. An adult female from Little Grand Canyon was taken from a burrow in a drier, less sheltered spot than the shelter caves of Ferne Clyffe State Park (J. Beatty, personal communication). *A. unicolor* is also apparently more abundant at each of these three localities than is *A. hadros.*

LIFE HISTORY

Males. Collecting data (Fig. 1) indicate that penultimate males molt to maturity during late summer or early fall and wander and mate during the first half of fall. Two mature males were collected on 13–14 September in their burrows shortly after the final ecdysis. Pitfall traps planted at Pine Hills by J. Nelson in 1967 collected one wandering male during the first week the traps were set out (7–14 October), nine males during the next week, none during the next week, three during the next week (27 October–3 November), and none during the next week, the final week traps were put out.

Females. The limited data (Fig. 2) hint that timing of brood development in *A. hadros* may be similar to that in *A. unicolor.* Second instar morphology is like that of *A. riversi.* The size of only one brood could be determined (Table 3).

BEHAVIOR

Burrow structure. The burrows were roughly tubular and completely lined with silk. The lining of several adult female and both adult male burrows were especially thick and white. Most burrows were widened slightly just below the entrance and at the bottom end (Fig. 35). Burrows of adult males averaged smaller than those of adult females (Table 6). Probably because of the pebbly soil, many burrows had abrupt curves, with the slope of the bottom end varying from vertical to horizontal.

Entrance structure. The entrances of only two adult females and two immatures were observed. The tubular silk lining of the burrow was extended slightly above the ground surface to form a very short and thin collar (Figs. 36–37). Soil particles were incorporated into the collars so that the external surface had the same texture and color as the surrounding soil surface. The height of each collar was quite strongly reduced at two opposing points on its circumference. When the collar is collapsed, the folding is concentrated at these two points, and the opposing higher sectors or flaps of the collar meet and overlap in the center along the line connecting the two reduced points.

Brood behavior. No egg sac remnants were present in the four burrows with second instar broods collected from Ferne Clyffe State Park. These spiderlings reacted quickly to stimuli and could move about rapidly. They were clustered in the bottom of two burrows, and were more scattered in the other two but retreated down to the burrow bottom as I exposed each burrow.

Molting behavior. The burrows of both recently matured males were heavily lined with silk. Both spiders were sufficiently sclerotized to be active. The recently shed exuviae had been pushed into the very bottom ends of the burrows and covered over with a thin layer of silk. Since both burrows were discovered by scraping the soil surface, I could not determine whether the closed collars had been sealed with silk.

Feeding behavior. Burrow entrances were closed during the daytime. Burrows of several immature *A. hadros* observed 90 minutes after nightfall had the collars open only a crack, while adjacent *A. unicolor* immatures had their collars wide open. Fragmented prey exoskeletons were packed into the bottom ends of a few burrows. Such trash from two immature burrows was examined and found to consist of ant and beetle parts.

Aliatypus californicus (Banks)

ECOLOGY

Geographic distribution and elevation range. West central California from the San Francisco Bay region to the Monterey Peninsula. 1000–2900 ft (300–880 m).

Habitat. I have collected only three specimens, all these near Felton, California, between 1000 and 1600 ft in or near aggregations of *Atypoides riversi. Actinoxia* burrows were also present but as uncommon as those of *A. californicus.* All burrows were found on steeply inclined road banks in rather dense mixed deciduous-coniferous forest (tan oak, pine, and some coast redwoods). The soil varied from clay to sandy loam, was quite rocky, and was dry at the surface.

The holotype specimen was collected at the side of a stream (Banks, 1896). Smith (1908) collected *A. californicus* in the foothills and mountains on both sides of the Santa Clara Valley, finding burrows most commonly along banks of streams and roads in "fine compact sandy soil." Occasionally burrows were found in "sandy adobe" soil. These banks with burrow aggregations "usually have little or no vegetation upon them other than short scattered moss." Smith found *A. californicus* "commonly associated with *Eutychides* [= *Actinoxia*] and *Atypoides* [*riversi*]."

LIFE HISTORY

Males. Smith (1908) collected the only two known males of *A. californicus* during October (Fig. 1), but failed to indicate whether they were taken from burrows or collected wandering.

Females. Smith (1908) observed that most burrows (at least of those found in exposed banks) were sealed shut from June to "the first rains in December." "None were found with sealed doors from the end of December to the end of April." At least some burrows in shaded stream banks were not sealed for such a long time. Such estivating behavior during the dry season may be common to other species of *Aliatypus.*

BEHAVIOR

Burrow structure. Smith (1908) states that "the burrow is comparatively long, [and] simple. . . ." "I have seen no evidence of branches of any type, nor any suggestions of extensions above the surface. The silk lining is so meagre as to be practically indiscernible. The burrows of small specimens are not easy to distinguish from those of certain mining bees, tiger beetles, etc. . . ." Gertsch (1949) notes that "the silken lining is quite thin, but thickens around the opening. . . ." I have observed only two burrows. One was an adult female burrow which was well lined with silk in the upper half but with very little or none in the lower half. The burrow was nearly straight, sloped downward with a burrow pitch of 15°, and the bottom end was somewhat enlarged. The other (immature) burrow was straight, sloped downward with a burrow pitch of 30°, was roughly of equal diameter its entire length, and was detectably lined with silk only near the entrance. (See Table 6 for dimensions.)

Entrance structure. Banks (1896) reported that the holotype burrow entrance was covered with a trapdoor. Smith (1908) observed that the entrance structure was a "simple trapdoor" constructed of silk and soil, sometimes with bits of moss or grass attached. Spiders inactive during the dry season had the trapdoors "plastered down firmly with soil." "Doors sealed up in this way are harder to see, as a rule, than when normally fastened at the hinge only." Smith gives the dimensions of two of the largest trapdoors he examined: 21 × 15 mm and 18 × 13 mm. Gertsch (1949) described the trapdoor as being "of the wafer type." I have observed the entrance of only one medium size immature burrow. The trapdoor was thin and waferlike but quite tough, and was joined broadly to the burrow lining by a wide hinge. The outside surface of the door matched the immediate ground surface, and the inside surface was silk continuous at the hinge with the silk lining of the burrow. The trapdoor was closed and the entrance sealed by a 1 cm thick hardened plug of soil just inside the door.

Trash disposal. Both burrows which I observed had fragmented prey rejectamenta packed into their bottom ends.

Aliatypus no. 1

ECOLOGY

Geographic distribution and elevation range. A small area in southern California between Riverside and Palm Springs. 1000–4000 ft (300–1200 m).

Habitat. A population of *A.* no. 1 was observed in a xeric habitat in the foothills of the Box Springs Mountains on the edge of Riverside, California. Burrows were scattered over the 30–80° inclines of ravine banks covered only with dry scattered vegetation of grass and shrubs. The dominant larger plants were wild buckwheat (*Eriogonum*) and sagebrush (*Artemesia*). The soil was chiefly orange sandy loam with a rather high content of decomposed granite. Two other genera of burrowing mygalomorph spiders (*Bothriocyrtum* and *Aptostichus*) were found in this same location and habitat.

LIFE HISTORY

Males. The data (Fig. 1) indicate that males of this species may wander and mate with the coming of humid weather in late fall or winter.

Females. Examination of the contents of four egg sacs containing first or second instar spiderlings indicates that the pattern of early postembryonic development in this species is similar to that in *Antrodiaetus unicolor.* The morphology of the embryonic cuticle, first instar, and second instar is also similar to that of *A. unicolor*, with the exception of those differences in the second instar that are present in older instars as well. The four brood records (Fig. 2) indicate that the cycle of brood development in this species may begin later than that of *Antrodiaetus unicolor* and other species of *Antrodiaetus* and *Atypoides.* The two first instar broods collected on 5 October and one of the first instar broods collected on 10 October were kept alive and had reached the second instar stage by the end of October. Brood sizes are given in Table 3.

BEHAVIOR

Burrow structure. The burrows of four adult females, several immatures, and one adult male were observed. They were tubular and relatively long (Table 6) and straight. Variation in diameter along their length was not recorded. The adult female burrows had a thick silk lining near the entrance and usually a thin silk lining over most of the rest of the burrow. The walls in the vicinity of the egg sac were more thickly lined with silk. Immature burrows were silk lined near the entrance but very thinly or not at all elsewhere. The burrows of two adult females sloped downward with pitches of 0–10°. The male burrow was considerably smaller than the adult female burrows.

Entrance structure. The burrow entrance is provided with a wafer type trapdoor (Figs. 38–39 and 54–55) composed of soil and silk and often particles of ground surface materials. The trapdoor of adult females is 1–2 mm thick. The outer surface is well camouflaged and the inner surface is silk lined, this lining being continuous with the burrow lining at the hinge. The hinge is almost as wide as the maximum diameter of the entrance. The rim of the burrow opening is usually flared outward slightly to form a narrow lip against which the trapdoor fits snugly when closed. Many of the spiders collected in September and early October had sealed their trapdoors shut with silk seals and/or soil plugs applied to the inside of the door. The adult male's trapdoor was sealed shut with silk applied to the inner surface of the door and the adjacent burrow wall.

Egg sac structure and position. The structure of the egg sac is poorly known. The thickness of the sac wall appears similar to that of *Antrodiaetus* and *Atypoides* egg sacs. The egg sac is apparently firmly and broadly attached to the burrow wall, and at least somewhat flattened, as in *Antrodiaetus* and *Atypoides* species. The sacs were positioned in the bottom of the burrow (Table 6).

Molting behavior. The penultimate exuvia of the nearly fully sclerotized adult male lay slightly broken up in the bottom end of the burrow. Its trapdoor was sealed shut with silk.

Feeding behavior. Broken prey cuticle was found in the bottom end of several burrows. Identifiable prey included several tenebrionid beetles, ants, and a mutillid wasp.

Aliatypus no. 2

ECOLOGY

Geographic distribution and elevation range. Southern California in the vicinity of Los Angeles. 500–2500 ft (150–760 m).

Habitat. A dense burrow aggregation of this species was found at Placerita State Park, California, on a north-facing road bank. Burrows of three adult males, five brooding females, and another adult female were found within a 0.2-m^2 area.

LIFE HISTORY

Males. Collecting records (Fig. 1) indicate that adult males of this species wander and mate during the wet season in late fall and in winter.

Females. An examination of the single first instar brood and the second instar broods indicates that the pattern of early postembryonic development is similar to that of *Antrodiaetus unicolor.* Almost all of the shed chorions examined contained the embryonic cuticle. The morphology of these stages is similar to that of *A. unicolor,* except for the larger rastellar macrosetae and retention of the anterior lateral spinnerets in *A.* no. 2. Brood records (Fig. 2), like those of *A.* no. 1, indicate that the cycle of brood development may begin later than in *Antrodiaetus unicolor.* Only one complete brood was collected (Table 3).

BEHAVIOR

Egg sac structure. The single preserved egg sac had a similar shape and the sac wall thickness appeared similar to that of *Antrodiaetus unicolor.*

Behavior of brooding females and broods. The spiderlings apparently emerge from the egg sac early in the second instar or possibly very late in the first. Only the first instar brood was still within the egg sac.

Aliatypus spp.

Several other *Aliatypus* populations have been sampled, but few natural history observations have been recorded. A few of these populations probably belong to the above pair of undescribed species; others represent new species. These samples are scattered widely in Southern California from Yosemite National Park south to the Los Angeles area. Their total elevation range is 1000–7000 ft (300–2130 m). Almost all samples were collected in dry nonforested habitats similar to those of *A.* no. 1 and *A.* no. 2. One population (possibly conspecific with *A.* no. 2) was found along the 30–60° incline of a 2-meter deep ravine in Water Canyon in the Tehachapi Mountains, California. Grasses and willow bushes (*Salix*) were the dominant vegetation. The soil was dark friable clay-loam that became humid at about 20 cm below the surface (on 7 September). Burrows of the ctenizid genus *Aptostichus* were present in the same ravine. All male records (Fig. 1) indicate that wandering and mating occur during the winter wet season. When observed, entrances have always been trapdoors.

Summary and Discussion

So many gaps exist in our present knowledge of these spiders that it is not possible to do much more than briefly summarize and discuss the above data where it is plentiful or of special interest.

ECOLOGY

Habitat. Throughout the major part of their ranges, the genera *Antrodiaetus* and *Atypoides* are clearly the most successful (in terms of abundance) mygalomorph spider genera. Apparently few other mygalomorph groups are so successfully adapted for life in the cool temperate zone. The different species of *Antrodiaetus* occupy a variety of habitats—at one end of the spectrum *A. unicolor* and *A. pacificus* are found in humid forest habitats and at the other end *A. montanus* lives in dry, often nonforested, habitats—but the genus is basically adapted to fairly humid forest or woodland habitats. In the northwestern United States, where a number of species are sympatric, there is evidence for habitat segregation among the closely related species *A. pacificus, A. hageni, A. montanus,* and *A. pugnax,* i.e., ecological isolating mechanisms may be operative.

There is considerable evidence (described above) that *A. hageni* is found in relatively dry unforested habitats that are often distinct from the more humid forest habitats of sympatric *A. pacificus* populations. These two species have not yet been collected together in mixed burrow aggregations. *A. montanus* occurs in unforested or thinly forested habitats usually too dry for *A. pacificus*. It apparently occurs in mixed populations with *A. pacificus* only in open montane forests such as at Crater Lake, Oregon. (This is apparently marginal habitat for both species.) In the eastern portions of Washington and Oregon, the low, riparian, deciduous woodland habitats of *A. pugnax* are usually separated by wide expanses of wheatland or sagebrush-grassland from the higher montane forest habitat of *A. pacificus*. Except for possible contact of these two habitats along streams in the foothills of mountains, these two species may be effectively separated in this region. However, in the Willamette River Valley and the lowlands to the north, both species have been collected at the same localities. (Adult males of both species have been collected in Douglas fir forest at Olympia, Washington, and in a single pitfall collection at Eugene, Oregon.) Apparently habitat segregation in this region is at least imperfect. I have yet to find mixed species populations of any pairing of *A. hageni*, *A. montanus*, and *A. pugnax*.

The species of *Atypoides* are, like most *Antrodiaetus* species, usually found in relatively humid forest or woodland habitats. Even though *Atypoides gertschi* is sometimes found in manzanita chaparral, it is found only where the subsurface soil is humid. All three species are sympatric with *Antrodiaetus* species. *Atypoides hadros* is commonly found in mixed species populations with *Antrodiaetus unicolor*, with no evidence yet of habitat segregation. Over much of its range *A. gertschi* is sympatric with *Antrodiaetus pacificus* and probably *Antrodiaetus montanus*. One or both of these species was often found in low numbers in *A. gertschi* aggregations. On the slopes of Mt. Shasta, California, above 5500 ft, only a single *Antrodiaetus* specimen was found among the dense *A. gertschi* populations, but, at 4950 ft at McBride Springs, *A. gertschi* and *Antrodiaetus* exhibited habitat segregation. *Antrodiaetus* (immature, probably *A. pacificus*) burrows were found only in the dark, humid, organically rich loam soil of the stream bank immediately below the spring in the heavy shade of a small dense stand of young fir and pine trees. *A. gertschi* burrows were present only in the volcanic "sand" soil (dry and loose at the surface, humid and packed below 5–7 cm depth) along the edge of the same stream in an extensive area of chaparral only 10–20 m downstream of the spring.

The habitats of *Aliatypus* species are poorly known, but are relatively dry and usually nonforested. Most species are found within the Californian Province as defined by botanists (Gleason and Cronquist, 1964) and experience the long annual dry season characteristic of southern California. *Aliatypus* species are found competing in the same habitats with several genera of Ctenizidae, the trapdoor spider family towards whose niche *Aliatypus* has converged.

LIFE HISTORY

Males. In most species of *Antrodiaetus* and *Atypoides*, the males emerge from their burrows, wander, and mate sometime during the summer and fall, primarily during the second half of summer and early fall (Fig. 1). One exception is *Antrodiaetus lincolnianus*, which apparently mates in early spring. Two other possible exceptions are *Antrodiaetus cerberus* and *Antrodiaetus roretzi*. The partly sympatric species *A. lincolnianus* and *Antrodiaetus stygius* appear to be separated by an effective temporal isolating mechanism. Other pairs of *Antrodiaetus* that are possibly separated in part by temporal isolating mechanisms are *A. pacificus* and *A. occultus*, *A. pacificus* and *A. cerberus*, and *A. occultus* and *A. pugnax*. The studied species of *Aliatypus* appear to mate during late fall or winter.

Climate appears to have an important influence on the time of wandering and mating. High elevation populations (*Antrodiaetus apachecus,* the Sierran populations of *Atypoides riversi,* and *Atypoides gertschi*) often tend to mate earlier than low elevation relatives. There seems to be considerable selective pressure for male wandering to occur during relatively humid periods. Some evidence exists for the triggering of *A. unicolor* male wandering by humid weather. *Aliatypus* species do not mate until the California wet season commences. Coastal populations of *Atypoides riversi* probably do not mate until the long dry season ends in the fall.

Females. The pattern of early postembryonic development appears to be similar in all three genera, although many species are unstudied. The timing of brood development in nature is reasonably well known for only one species, *Antrodiaetus unicolor* (Fig. 2). The small amount of data for a few other species of *Antrodiaetus* and *Atypoides* indicate that these have a somewhat similar schedule of brood development. In some species of *Aliatypus* the brood cycle may be shifted slightly toward the beginning of the winter wet season, but more information is needed. Some species (*Antrodiaetus pugnax, Antrodiaetus stygius,* and *Aliatypus californicus*) may commonly seal their burrow entrances for rather long periods of time during the summer. Such inactivity may be primarily an adaptation to prevent desiccation during dry periods, or possibly to reduce parasitism.

Antrodiaetus unicolor and *Antrodiaetus pacificus* have markedly larger mean brood sizes than any other species of *Antrodiaetus* and *Atypoides* studied (Table 3). This ability to produce large broods may be an important factor in the success of these two abundant species. *Aliatypus* is poorly studied. The egg size of *A. unicolor* and *A. pacificus* averages smaller than that of the other species studied (Table 4). It would seem advantageous for an individual spider to be able to reduce egg size as much as possible without reducing offspring survival ability and thereby maximize the egg number. Why have *A. unicolor* and *A. pacificus,* the adult females of which average slightly smaller than *Antrodiaetus montanus* and larger than *Antrodiaetus pugnax* and *Atypoides riversi,* been most successful in reducing egg size? Perhaps a lower probability of egg and spiderling desiccation in their more humid habitats is an important factor. Much more and other kinds of data are needed to attack this problem effectively.

BEHAVIOR

Burrow structure. There are numerous factors such as substrate environment and body size that cause intraspecific variation in burrow shape and size and in the condition of the burrow lining. However, some aspects of burrow structure are rather constant within species and show interspecific differences. (The three *Atypoides* species can be easily distinguished from each other by differences in burrow and entrance structure.) The burrows of all studied *Antrodiaetus* and *Atypoides* species are roughly tubular and more or less enlarged at the bottom end and just below the entrance, with the exception of *Atypoides riversi,* in which the very bottom end of the burrow is usually narrowed. *Aliatypus* is poorly studied. Adult female burrow length varies considerably within species, but species of smaller body size (*Antrodiaetus pugnax, Atypoides hadros*) tend to have shorter burrows, and those in habitats with particularly dry soil (*Antrodiaetus montanus, Aliatypus* no. 1) apparently tend to have longer burrows (Table 6). All studied species line their burrows with silk, with the thickest lining in and near the entrance, where the substrate is usually the least stable. Some species frequently have very little lining silk in the rest of the burrow.

The burrow pitches of the studied species in all three genera fall within 0–35° and average between 0° and 15°. Only rarely do the burrows of any studied species slope upward from the entrance. The probable adaptive significance of such a nearly perpendicular burrow inclination is that as much of the burrow as possible is removed from the unstable environment of the surface soil. *Atypoides gertschi* burrows tend to turn toward the horizontal at their end. Burrow construction behavior has been observed in only one species, *Antrodiaetus unicolor.* More complete studies of this behavior, particularly of entrance construction, are essential for tracing the evolution of burrow and entrance structure in the Antrodiaetidae.

Entrance structure. All studied species of *Antrodiaetus* have flexible collar entrances that stand erect when open. However, the collar of *Antrodiaetus roretzi* is apparently markedly reduced at two opposing sectors so that it consists essentially of two opposing flaps. *Atypoides hadros* and *Atypoides gertschi* both have flexible collar entrances, but that of *A. gertschi* is rather thick, and when opened, collapses outward instead of remaining erect. *Atypoides riversi* constructs a rigid elongate collar or turret, the opening of which is normally kept open both day and night. All studied species of *Aliatypus* construct wafer type trapdoors.

Probably the two chief functions of the entrance closure of these spiders are to prevent the entry of predators and parasites (by providing camouflage and structural resistance) and to help maintain a favorable environment within the burrow (by preventing rain and runoff from entering and by maintaining higher humidity and moderate temperature). Without more behavioral and ecological data, it is difficult to say what special functional advantages each type of closure mentioned above has. The trapdoor closes automatically when the spider retreats from the entrance, and probably a trapdoor more effectively seals out external climate and flooding than a collar. Perhaps the *Aliatypus* trapdoor originated as a key adaptation for relatively unsheltered habitats in climates such as that of southern California, where occasional torrential rainfall with runoff and flooding and where long dry summers are characteristic. The possible functional significance of the turret of *Atypoides riversi* is particularly puzzling. Possibly it involves an enlargement of the prey sensing surface area. Possibly its rigidity and height serve to protect the burrow during runoff in heavy rain. A better understanding of the special functions of these closure types is needed for a clearer understanding of their evolutionary history.

I strongly suspect that both the turret entrance of *Atypoides riversi* and the double flap collar of *Antrodiaetus roretzi* have been derived from collar entrances resembling those of the other species of these two genera. It is possible that the trapdoor entrance of *Aliatypus* has been derived from a collar via the development of a dominant flap. It presently seems just as likely that both this trapdoor and the collar were derived independently from a simpler, more generalized ancestral type of entrance. It seems much less likely that the collar has been derived from a trapdoor entrance.

There appear to be two methods (perhaps not always distinct) used for sealing an entrance: 1) sealing inside with silk only, or 2) sealing inside with a plug of soil and usually silk combined. Both methods have been observed in each of several species (*Antrodiaetus unicolor*, *Antrodiaetus pacificus*, and *Aliatypus* no. 1). The first method is commonly employed by *Antrodiaetus unicolor* and *Atypoides riversi*, the second method by *Antrodiaetus pugnax*, *Antrodiaetus stygius*, *Aliatypus californicus*, and *Aliatypus* no. 1. Sealing is performed by molting spiders, some brooding females, and spiders which appear to become somewhat inactive during part of the summer. Both sealing methods, particularly the second, probably considerably improve the climate control and predator and parasite defense functions hypothesized above for the unsealed entrance closure.

Egg sac structure and position. Egg sac structure is similar in all studied species of *Antrodiaetus* and *Atypoides*, whereas in *Aliatypus* it remains undescribed. Egg sac position in the studied species of *Antrodiaetus* and *Atypoides* (Table 6) often varies considerably within species, but in all these species, except possibly *Atypoides gertschi,* the egg sac is usually positioned between 0.4 and 0.8 of the distance down the burrow and usually on the ventral sector of the wall. The only species of *Aliatypus* studied (*A.* no. 1) appears to position its egg sac at the very bottom of the burrow. Those species found in habitats with the dryest soil (*Antrodiaetus montanus, Antrodiaetus pugnax*, and *Aliatypus* no. 1) appear to place their egg sacs deepest in the burrow, probably because of the greater humidity there.

Brood behavior. In studied species of all three genera, the brood emerges from the egg sac either in the second instar or late in the first instar. There is substantial evidence that in *Antrodiaetus unicolor* the second instar brood overwinters in the parental burrow and disperses in the spring. This might greatly increase the winter survival of offspring of species living in areas with cold winters. The second instar of all studied species is quite active, morphologically equipped for most adult functions, and, in *A. unicolor* at least, is capable of constructing burrows.

Molting behavior. In *Antrodiaetus unicolor, Antrodiaetus pacificus*, and *Atypoides riversi,* molting commonly occurs in sealed burrows and is performed on the burrow wall above the bottom of the burrow. After ecdysis the spider rests in the bottom end while sclerotization proceeds. Eventually the exuvia is removed from the burrow wall and packed into the bottom end of the burrow. Data for other species in all three genera appear to fit this scheme. Scanty data indicate that *Antrodiaetus roretzi* may behave differently.

Defensive behavior. When prodded, several species of *Antrodiaetus* and *Atypoides riversi* assume an aggressive defensive posture similar to that of *Antrodiaetus unicolor* at the bottom end of the burrow. Other species of these two genera and *Aliatypus* are unstudied. The bottom end of the *A. riversi* burrow is uniquely narrowed, resulting in a tighter fit for the abdomen when in this defensive posture, and is thus probably more effective protection. Probably pompilid wasps and possibly centipedes are two important predators against which such defensive behavior is employed.

Feeding behavior. In the few species of *Antrodiaetus* and *Atypoides* studied, adults forage chiefly at night, and the foraging posture of each species appears similar. Considerable evidence for *Antrodiaetus unicolor* and *Atypoides riversi* indicates that prey is detected solely by substrate vibrations. *A. unicolor* appears to be an unselective predator. Many species commonly pack fragmented prey exoskeletons into the bottom end of the burrow. Very little data exist on the feeding behavior of *Aliatypus.*

Mating behavior. Evidence from several species of *Antrodiaetus* and *Atypoides* indicates that males wander in search of mates only at night. Certainly such nocturnal behavior would reduce the threat from visual predators and desiccation. Presumably at least the first stages of courtship or mating also take place then, with vision playing no part. Mating behavior has been observed only once, in *Atypoides riversi.* However, with this observation, with knowledge of antrodiaetid male morphology, and with observations on the functional morphology of male mating structures in other groups of mygalomorph spiders, it is possible to form a predictive hypothesis about mating behavior in the Antrodiaetidae.

In *Atypoides riversi,* the cheliceral apophyses of the male are placed between the outspread chelicerae of the female to hold her in position during mating. The similarly well-developed male cheliceral apophyses of the other *Atypoides* species almost certainly perform the same function. Perhaps the male first legs aid in holding the female, but only *A. hadros* males possess a fairly strongly modified first leg (with macrosetae grouped at the proximal end of the tibia).

Males of all species of *Antrodiaetus* lack cheliceral apophyses. (The anterior-dorsal prominence on the chelicerae of *Antrodiaetus* males is apparently a vestigial cheliceral apophysis.) However, most species possess first leg modifications analogous to the tibial spurs and other first leg structures, which, in males of many mygalomorph groups, function in holding the female during mating (for example see Buchli, 1962; Petrunkevitch, 1911a; and Todd, 1945). In the *unicolor* species group and in *Antrodiaetus roretzi,* there are clusters of strong macrosetae on the prolateral and, often, ventral surfaces of the male first tibia and sometimes a sharp bend in the male first metatarsus. Presumably these structures contact some part of the female and hold her in position during mating. The male first legs of the *lincolnianus* species group are only weakly modified, possessing a presumably homologous group of enlarged setae on the prolateral surface of the first tibia. Probably *Antrodiaetus* males hold the females during mating primarily with the modified first legs. The weakly modified chelicerae are probably less important.

Males of all *Aliatypus* species lack cheliceral apophyses and possess no special holding modifications on their legs. However, the pedipalps, unlike those of the other two genera, are extremely elongate. Perhaps in *Aliatypus* the male, when mating, contacts the female only lightly at a distance and reaches the greater distance to her genital opening with his long pedipalps. Studies of mating behavior should receive high priority among the different approaches used to unravel the evolutionary history of the Antrodiaetidae and the other atypoid mygalomorph families.

TABLE 1. TIMING OF BROOD DEVELOPMENT IN *ANTRODIAETUS UNICOLOR* POPULATIONS. (The number of broods collected in a given developmental stage at each locality are recorded chronologically by collection date.)

Date		Locality	Large maturing eggs in abdomen	Eggs in egg sac	Hatching	First instar	First ecdysis	Second instar
April	1	Ohio, Adams Co.	1					
May	18–19	W. Va., *H*	2					
	20	W. Va., Pocahontas Co.	1					
June	11–27	Ala., *R*	7					
July	2	W. Va., Raleigh Co.		1				
	6	Ohio, *B*		2				
	21–22	Ky., *K*		7				
	23–25	Tenn., *O*	2	18	4	5		
	27–28	Ala., *R*	1	3				
	29	Ga., Murray Co.			1			
	31	Ga., Towns Co.		1				
Aug.	2–3	N. C., *P*			4	10		
	7–8	N. C., *N*		2				
	14–16	W. Va., *C*			3	4	1	3
	21–23	Va., *I*				3	2	5
	25–26	Va., *J*				2	4	9
	28–29	N. C., *M*					1	9
	31	Tenn., *L*						2
Sept.	1	Tenn., *O*				2		7
	5–7	Ala., *Q*				6	1	22
	11	Ark., Stone Co.						1
	14–16	Ill., *F*						6
	22	Ohio, *B*						3
Dec.	2–3	Ala., *Q*						5

TABLE 2. BROOD SIZE (NUMBER OF OFFSPRING PER BROOD) OF *ANTRODIAETUS UNICOLOR* POPULATION SAMPLES.

Sample	N (broods)	Range	Mean	Std. dev.
B	2	127–155	141.0	
C	9	79–185	120.2	±36.5
I	4	90–209	127.0	
J	5	99–318	189.0	±87.1
K	6	84–241	142.9	±54.2
M	1	102		
N	2	111–154	132.5	
O	31	38–236	144.1	±49.8
P	14	96–256	169.8	±52.3
Q	7	66–125	100.4	±18.6
R	3	114–160	134.6	

TABLE 3. BROOD SIZE (NUMBER OF OFFSPRING PER BROOD) OF ANTRODIAETID SPECIES.

	N (broods)	Range	Mean	Std. dev.
Antrodiaetus				
unicolor	87	38–383	145.7	±57.0
robustus	2	86–94	90.0	
pacificus	4	107–328	192.2	
pugnax	8	40–75	52.1	±12.1
montanus	1	78		
stygius	1	79		
Atypoides				
riversi (coastal)	7	43–80	63.1	±13.5
riversi (Sierran)	1	81		
gertschi	1	78		
hadros	1	80		
Aliatypus				
sp. no. 1	3	66–104	85.0	
sp. no. 2	1	139		

TABLE 4. EGG SIZE OF ANTRODIAETID SPECIES.
(Ten eggs measured in each brood.)

	N (no. of broods)	Egg diam. in mm		Time (months) in 80% EtOH between collecting and measurement
		Range	Mean	
Antrodiaetus				
unicolor	15	1.02–1.75	1.30	12–28
pacificus	3	1.13–1.46	1.32	9
pugnax	8	1.20–1.58	1.44	9
montanus	1	1.78–1.95	1.81	9
Atypoides				
riversi (coastal)	2	1.54–1.73	1.63	5
riversi (Sierran)	1	1.36–1.51	1.47	5

TABLE 5. BURROW DIMENSIONS AND EGG SAC POSITION OF *ANTRODIAETUS UNICOLOR* POPULATION SAMPLES. (Only adult female or adult or penultimate male burrow dimensions included. Sample size, range, and mean given for each sex of each sample. Burrow length is length in cm of longitudinal axis of burrow from ground surface to bottom end. Entrance diameter is maximum inside diameter in mm of burrow entrance opening. Egg sac position is a ratio: length of longitudinal axis of burrow from ground surface to upper end of egg sac/burrow length.)

Sample		Burrow length			Entrance diam.			Egg sac position		
B	♀	19	14–25	19.6	18	11–17	13.3	3	0.13–0.56	0.28
	♂	2	16	16.0	2	8–9	8.5			
C	♀	21	15–30	20.7	14	10–18	13.9	8	0.07–0.78	0.21
	♂	5	14–24	18.4	1	9				
Clifty Falls, Ind.	♀	2	27–38	32.5	2	12–17	14.5			
D	♀	9	11–29	19.5	9	11–20	14.7			
Grandview St. Pk., W. Va.	♀	2	13–19	16.0	2	9–11	10.0	1	0.38	
F	♀	9	14–30	20.3	6	10–13	12.0			
	♂	2	10	10.0	1	10				
I	♀	29	12–30	20.4	17	12–16	13.8	7	0.11–0.67	0.33
	♂	9	6–15	10.3	2	9–10	9.5			
J	♀	37	15–38	24.6	30	12–20	15.1	8	0.05–0.76	0.34
K	♀	14	14–31	20.9	10	12–17	14.7	7	0.06–0.72	0.49
L	♀	4	17–36	23.7	3	12–16	14.3			
	♂	1	4							
M	♀	20	10–30	20.9	10	11–15	12.9	3	0.56–0.67	0.61
N	♀	3	11–18	15.3	2	11–13	12.0	2	0.56–0.73	0.64
O	♀	48	9–33	20.6	45	11–14	12.5	31	0.48–0.83	0.66
	♂	1	15							
P	♀	35	10–29	20.9	22	11–15	13.5	15	0.08–0.75	0.40
	♂	6	11–16	14.0						
Q	♀	35	10–29	20.1	22	10–14	12.3	12	0.35–0.85	0.65
R	♀	8	16–33	24.0	8	11–13	11.8	3	0.48–0.67	0.59
Blanchard Springs, Ark.	♀	2	11–21	16.0						
	♂	1	8							

TABLE 6. BURROW DIMENSIONS AND EGG SAC POSITION OF ANTRODIAETID SPECIES. (Variables and samples defined as in Table 5. Turret height is length in mm of longitudinal axis of turret from ground surface to top of turret.)

		Burrow length		Entrance diam.		Turret height		Egg sac position	
Antrodiaetus									
unicolor	♀	307	9–38(21.2)	226	9–20(13.4)			101	.05–.85(.51)
	♂	28	4–24(12.7)	6	8–10(8.8)				
robustus	♀	5	18–34(26.8)	4	10–13(11.3)			2	.67–.80(.74)
pacificus	♀	22	16–44(27.6)	18	11–13(12.3)			3	.13–.67(.48)
	♂	8	14–36(24.4)	4	10–11(10.3)				
pugnax	♀	13	9–23(13.8)	12	7–13(9.0)			8	.47–.85(.78)
	♂	2	7–9 (8.0)	2	8 (8.0)				
montanus	♀	3	31–46(38.3)	2	14 (14.0)			1	.71
hageni	♀	2	22–40(31.0)	1	13				
	♂	2	22–32(27.0)						
stygius	♀	3	20 (20.0)					2	.60 (.60)
	♂	2	14–16(15.0)						
roretzi	♀	?	10–15 —from Yamamoto (1942)						
	♂	2	6–10(8.0)—from Yamamoto (1942)						
Atypoides									
riversi (coastal)	♀	11	15–32(23.8)	8	11–14(12.6)	10	13–60(31.8)	8	.43–.59(.50)
	♂	5	18–21(19.8)						
riversi (Sierran)	♀	10	18–27(21.4)	8	9–14(11.3)	10	5–25(14.7)	1	.47
	♂	4	8–20(16.5)						
gertschi	♀	15	18–36(29.6)	13	13–16(14.0)			1	.25
hadros	♀	5	8–15(11.2)	2	9–10(9.5)				
	♂	2	7–8 (7.5)						
Aliatypus									
californicus	♀	3	16–25(19.0)—2 measurements from Smith (1908)						
sp. no. 1	♀	4	31–46(38.0)	4	11–13(12.0)			4	.90–.95(.92)
	♂	1	23	1	7				

TABLE 7. THE INSTAR COMPOSITION OF PRE-EMERGENT, EMERGING, AND EMERGED (FROM EGG SAC) BROODS OF *ANTRODIAETUS UNICOLOR* POPULATION SAMPLES. (Numbers represent number of broods in each category in each sample.)

Instar of brood	Brood entirely within egg sac			Brood emerging from egg sac			Brood entirely outside egg sac		
	1	1+2	2	1	1+2	2	1	1+2	2
Sample									
B									2
C	5	1		1	1				3
F									6
I	3				1	1		1	4
J	1	2		1	2	1			8
L									2
M					2				8
O	10			1					7
P	13			1					
Q	6	1				3			24
Total	38	4		4	6	5		1	64

TABLE 8. FREQUENCY OF BROODING FEMALES WITH SEALED AND UNSEALED BURROW ENTRANCES IN *ANTRODIAETUS UNICOLOR* POPULATION SAMPLES. (Asterisk signifies that majority of females had collar open or collar was open and spider was also in foraging posture.)

	Before brood emerges from egg sac		After second instar spiderlings begin emerging from egg sac	
Sample	Unsealed	Sealed	Unsealed	Sealed
B		3		2
C		2		1
F			1	2
I				1
J		2	3	6
K	1	1		
L			2	
M				3
N		1		
O	32*			6
P	1			3
Q	4*	2	14*	4
R	4*			

TABLE 9. RECORDS OF POMPILID WASP PREDATION ON *ANTRODIAETUS UNICOLOR*.

Locality	Date	Developmental stage of wasp: Egg	Early instar larva	Larva in cocoon	Abandoned cocoon	Soil plug in burrow
Summers Co., W. Va.	July 3			1		?
Jefferson Co., Ind.	July 17	1	1			no
D	July 20	1				no
R	July 27			1		yes
Towns Co., Ga.	July 31				1	
N	Aug. 7				1	
C	Aug. 14–16		1	7		yes—4, no—4
J	Aug. 25	1				yes
M	Aug. 28			1		yes
Q	Sept. 6	1				no
Johnson Co., Ark.	Sept. 10			1		no

TABLE 10. PREY FOUND IN *ANTRODIAETUS UNICOLOR* BURROWS.

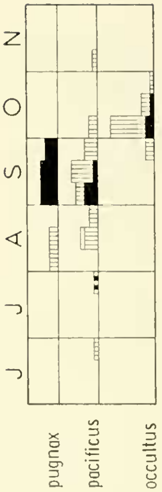
(Numbers indicate in how many of 102 burrows each prey taxon was found. The great majority of these are prey rejectamenta records; very few are records of freshly killed prey.)

Ants (Formicidae)	65
Beetles (Coleoptera)	64
Millipedes (Diplopoda)	11
Flies (Diptera)	4
Spiders (Araneae)	4
Harvestmen (Opiliones)	4
Sow bugs (Isopoda)	4
Snails (Gastropoda)	3
Wasps (Vespidae and Scolioidea)	2
Crickets (Gryllidae)	1
Caterpillars (Lepidoptera: Sphingidae)	1

2


M
A
M
J
J
A
S
O
N
D
Antrodiaetus
unicolor
robustus
pacificus
pugnax
montanus
hageni
cerberus
lincolnianus
stygius
Atypoides
riversi 1
gertschi
hadros
Aliatypus
no. 1
no. 2

3


J
J
A
S
O
N
pugnax
pacificus
occultus

1

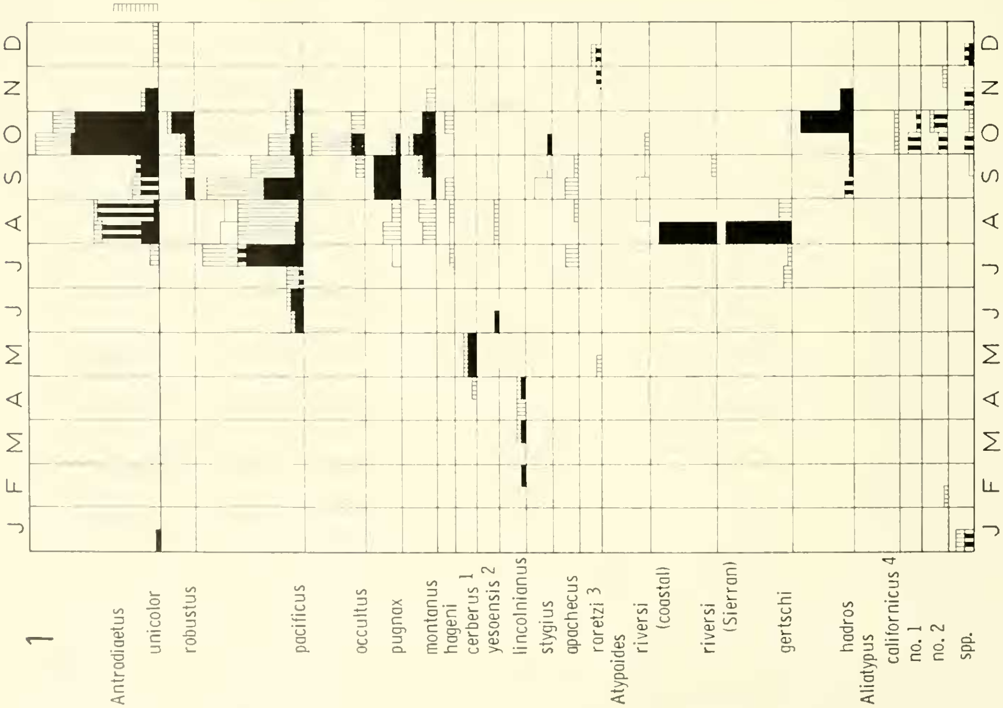
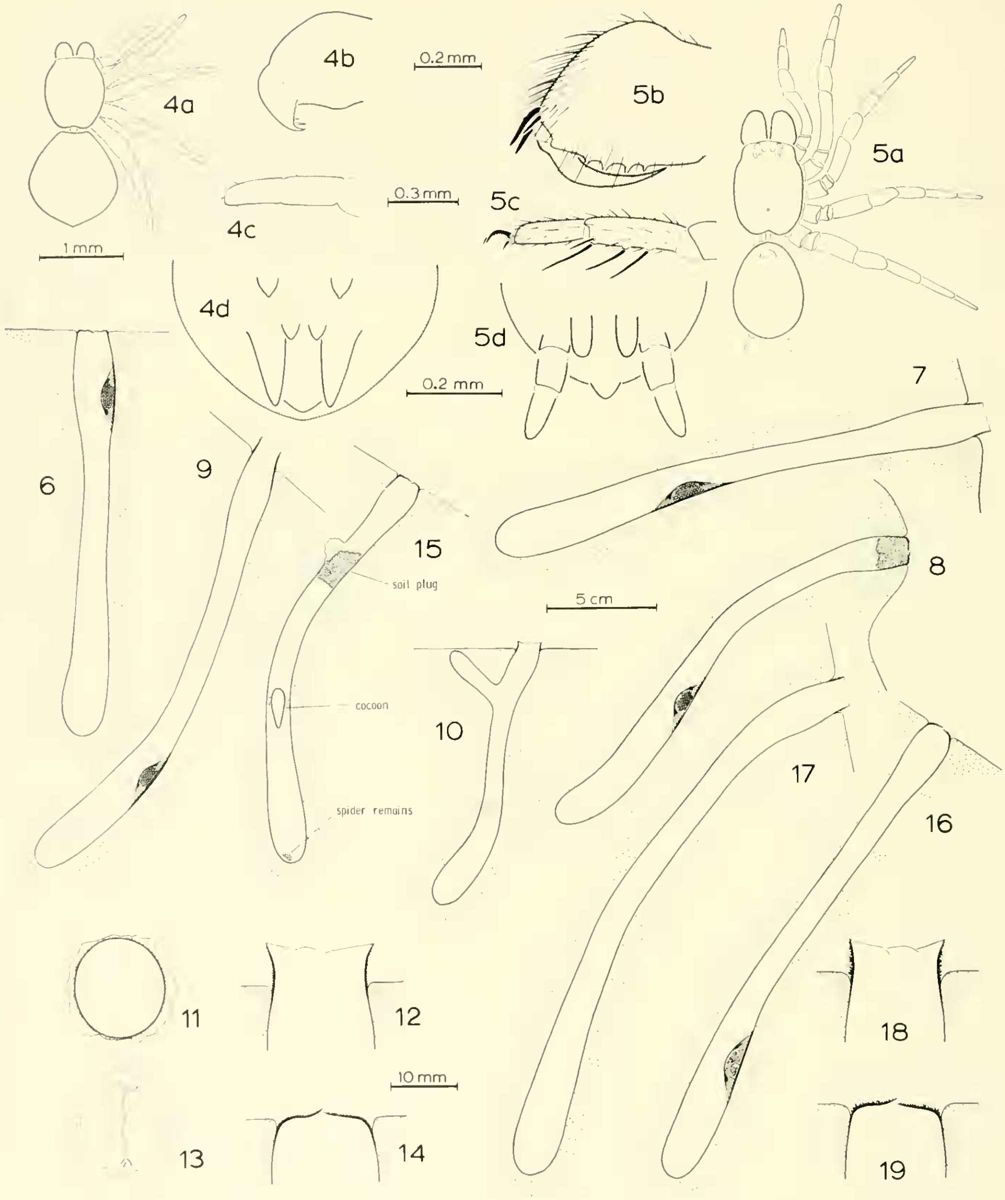
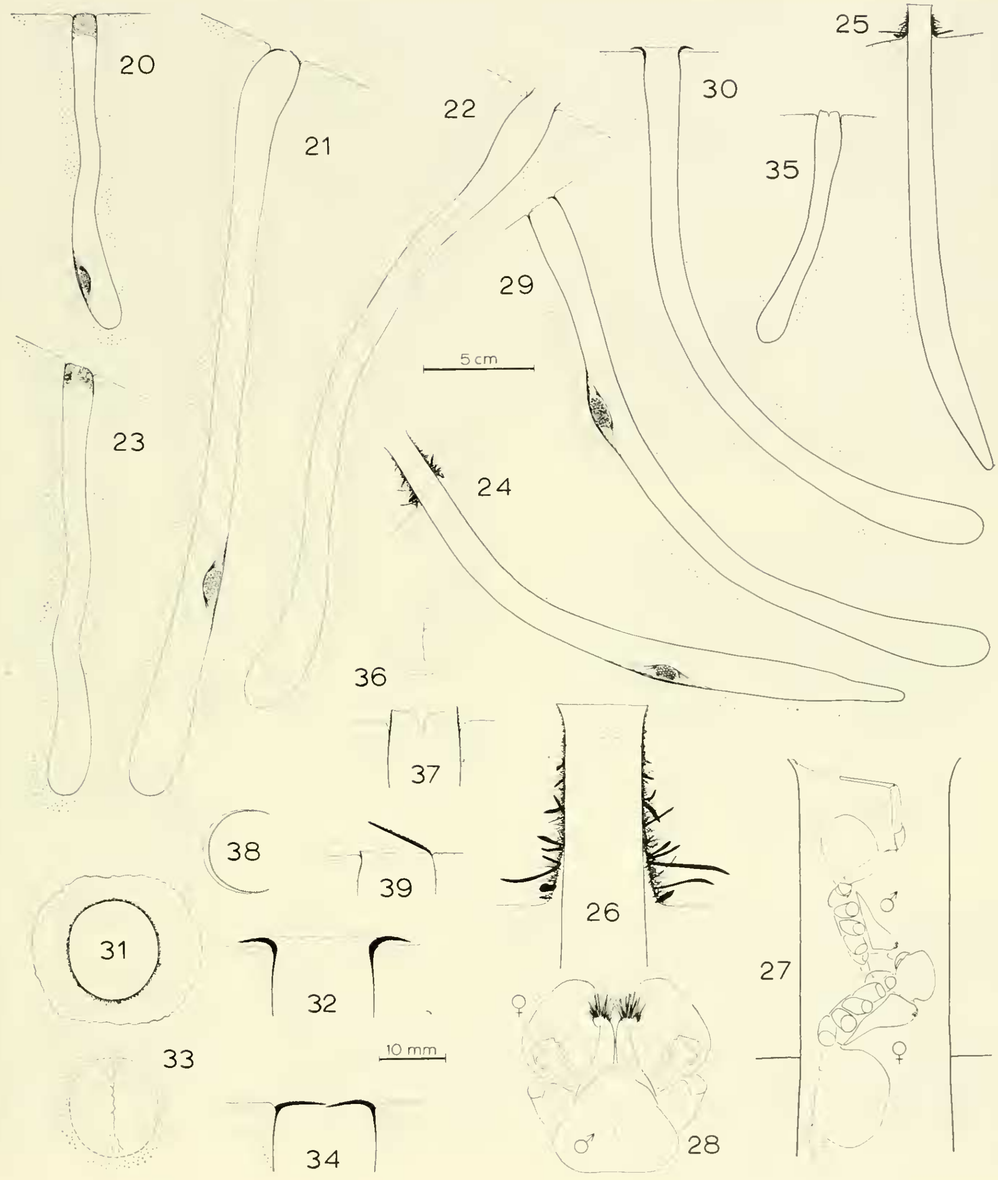

J
F
M
A
M
J
J
A
S
O
N
D
Antrodiaetus
unicolor
robustus
pacificus
occultus
pugnax
montanus
hageni
cerberus 1
yesoensis 2
lincolnianus
stygius
apachecus
roretzi 3
Atypoides
riversi (coastal)
riversi (Sierran)
gertschi
hadros
Aliatypus
californicus 4
no. 1
no. 2
spp.

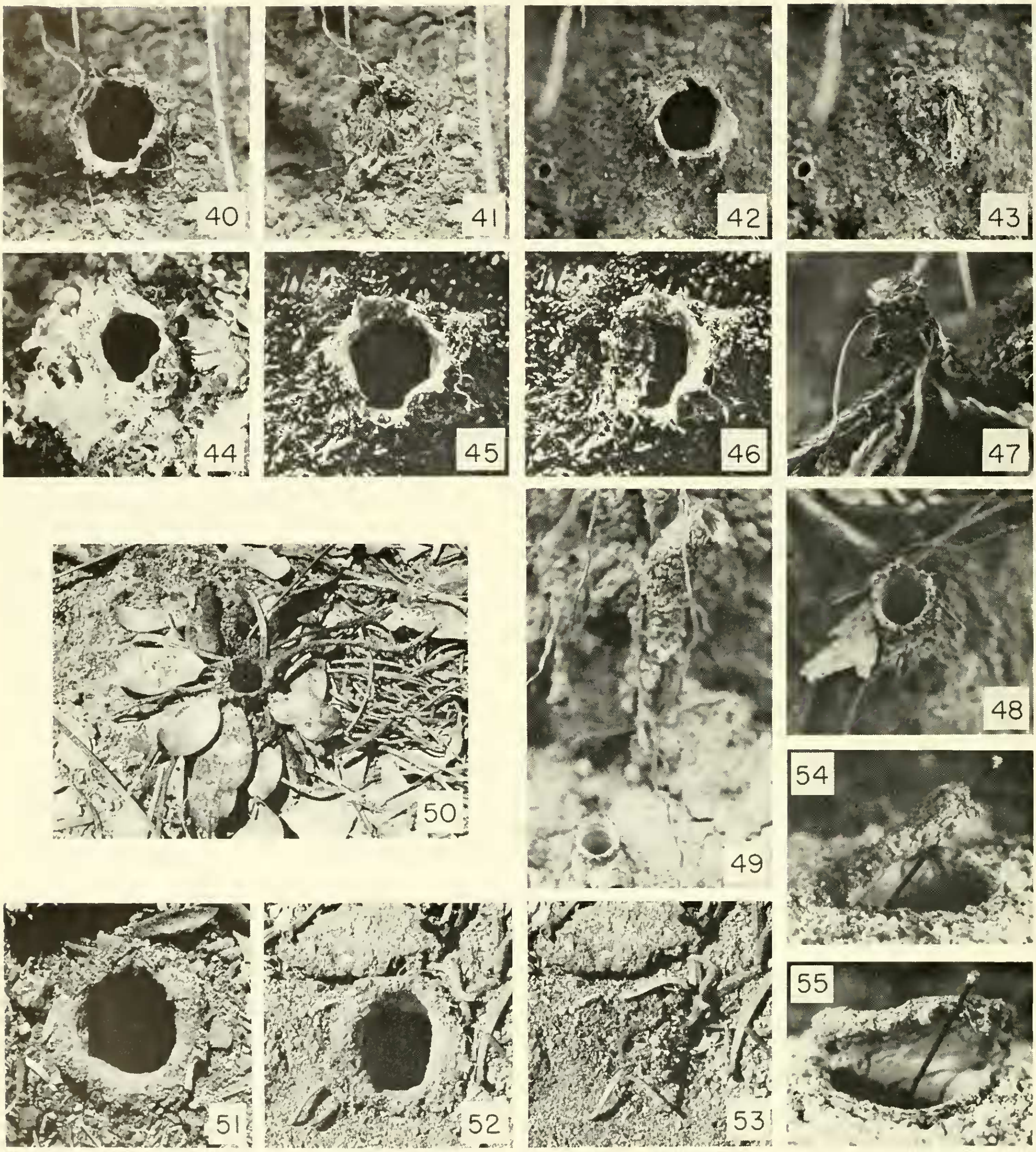
Figure 1. Collection dates of adult male antrodiaetids. Records grouped into ½ month periods. One unit of vertical scale represents one male. Solid black represents adult male collected after leaving its burrow. Two vertical bars represent adult male collected within its burrow before abandoning it. Vertical lines represent adult male collected either before or after leaving its burrow; inadequate data accompanies specimen. Empty rectangle represents date on which a male, collected in the penultimate instar, molted to maturity in captivity. All records are from examined specimens with the following exceptions indicated by superscript numbers: (1) 3 records from W. Ivie (personal communication), (2) June record is holotype collection date (Uyemura, 1942), (3) November record and one December record from Yamamoto (1942), (4) Both records from Smith (1908). Figure 2. Timing of brood development in antrodiaetid species. Collection dates and developmental stages of broods collected in the field. Records grouped into ⅓ month periods. One unit of vertical scale represents one brood. Broods in the form of large maturing eggs within abdomen are represented by an empty rectangle, broods consisting of eggs in egg sac by vertical lines, hatching broods by crosshatching, first instar broods by stippling, broods during first ecdysis by 2 vertical bars, and second instar broods by solid black. Note: (1) All *Atypoides riversi* broods are from coastal populations except for a single Sierran brood collected in the first ⅓ of August. Figure 3. Collection dates of adult males of *Antrodiaetus occultus*, *Antrodiaetus pacificus*, and *Antrodiaetus pugnax* in the Willamette and Umpqua River valleys from Roseburg, Ore., north to the Columbia River. Same symbols and scale as in Fig. 1. Records grouped into ⅓ month periods.



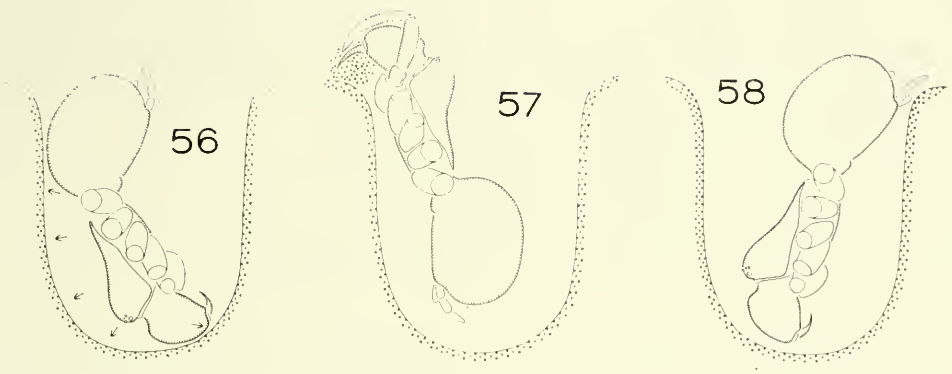
Figures 4–5. Early instars of *Antrodiaetus unicolor*. 4. First instar. 4a. Dorsal view. 4b. Chelicera, retrolateral view. 4c. Leg I metatarsus and tarsus, retrolateral view. 4d. Spinnerets and anal tubercle, ventral view. 5. Second instar; same views and scales as in Fig. 4. Figures 6–15. *Antrodiaetus unicolor* burrow structure. 6–9. Adult female burrows; *P*, *J*, *Q*, and O respectively. 10. Immature burrow, *D*. 11–14. Burrow entrance. 11–12. Open collar, frontal and sagittal views. 13–14. Closed collar, same views. 15. Burrow attacked by pompilid wasp, C. Figures 16–19. *Antrodiaetus pacificus* burrow structure. 16–17. Adult female burrows; *I* and *U* respectively. 18–19. Open and closed collar, sagittal view. (5 cm scale for burrows. 10 mm scale for collars.)



Figures 20–23. Adult female burrows of *Antrodiaetus* spp. 20. *A. pugnax*, *B*. 21. *A. montanus*; Pocatello, Ida. 22. *A. hageni*; Trail, B. C. 23. *A. stygius*, paratype. Figures 24–28. *Atypoides riversi*. 24–25. Adult female burrows; *D* and *I* respectively. 26. Open turret, sagittal section. (Modal form for coastal population. Dotted line indicates form of closed turret.) 27–28. Mating posture observed at G. (Drawn from field sketch and notes.) 27. Lateral view. 28. View looking down burrow. Figures 29–34. *Atypoides gertschi* burrow structure. 29–30. Adult female burrows; *N* and *O* respectively. 31–32. Open collar, frontal and sagittal views. 33–34. Closed collar, same views. Figures 35–37. *Atypoides hadros* burrow structure. 35. Adult female burrow; Ferne Clyffe St. Pk., Ill. 36–37. Collar of same burrow. 36. Closed, frontal view. 37. Open, sagittal view. Figures 38–39. *Aliatypus* no. 1 adult female burrow entrance; frontal and sagittal views with trapdoor open. (5 cm scale for burrows. 10 mm scale for entrances.)



Figures 40–55. Antrodiaetid burrow entrances (adult females only). 40–43. *Antrodiaetus unicolor*. 40–41. *J*, collar open and closed. 42–43. *Q*, collar open and closed. 44. *Antrodiaetus pacificus*; *U*, collar open. 45–46. *Antrodiaetus hageni*; Trail, B. C. 45. Collar fully open. 46. One lateral sector of collar collapsed by author. 47–50. *Atypoides riversi*. 47. *D*. 48. *I*. 49. *D*. 50. *I*. 51–53. *Atypoides gertschi*. 51. *O*, collar open. 52–53. *N*, collar open and closed. 54–55. *Aliatypus* no. 1; Riverside, Calif. Trapdoor propped open.



Figures 56–58. Drawings of *Antrodiaetus unicolor* burrow construction behavior. Sketched from frames of 16 mm movie film. 56. Burrowing. Arrows indicate general direction of forces produced by legs and chelicerae against cell wall. 57. Releasing load of soil onto rim of cell opening. 58. Silk application.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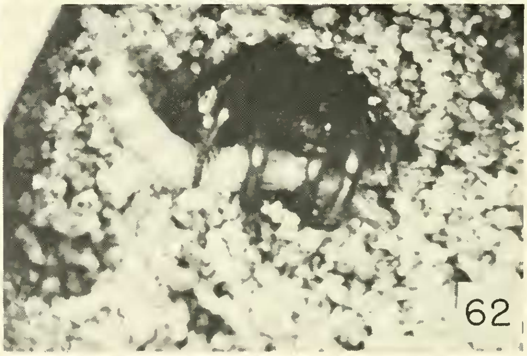
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Figures 56–58. Photos (16-mm movie frames) of *Antrodiaetus unicolor* burrow construction behavior. 56. Burrowing. 57. Releasing load of soil onto rim of cell opening. 58. Silk application. Figures 59–62. *Antrodiaetus unicolor* prey capture behavior. 59. Foraging posture (Photo by R. Ball). (Figs. 60–62 are 16-mm movie frames.) 60. Initial contact with prey (*Tenebrio* larva) at end of lunge from burrow entrance. 61. Fangs imbedded in prey. 62. Spider retreating into burrow with prey.


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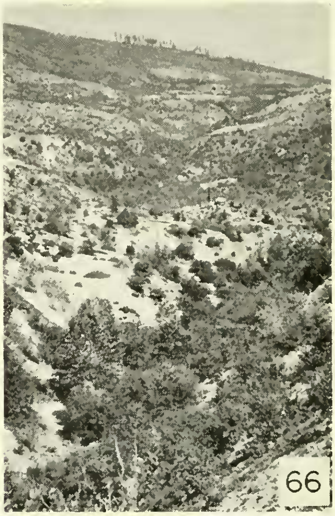
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Figures 63–68. Habitat photos. 63. Conifer forest habitat occupied by *Antrodiaetus pacificus* in Cascade Mtn. Range near *L*. 64. Riverbank woodland habitat occupied by *Antrodiaetus pugnax* at Lewis and Clark St. Pk., Wash. 65. Juniper-sagebrush habitat occupied by *Antrodiaetus montanus* at Pocatello, Ida. 66. Nonforested habitat occupied by *Antrodiaetus hageni* at Trail, B. C. 67. Tan oak-pacific madrone forest habitat occupied by *Atypoides riversi* at *D*. 68. California red fir habitat occupied by *Atypoides gertschi* at 7,400 ft at *N*.

TAXONOMIC METHODS

Analysis of Variation

I have approached the species level taxonomy of *Antrodiaetus* with two principal and interrelated aims: to discover morphological characters of high value in distinguishing between species, and to study geographic variation. Difficulty in achieving the first goal in many groups of mygalomorph spiders (including the Antrodiaetidae) is primarily a result of the relatively simple morphology of the male palpus and female genitalia, the difficulty of obtaining samples of adequate size, and the instar heterogeneity (and therefore greater variation) of adult female samples. The second difficulty has been overcome for many antrodiaetid species and the third has been reduced by the use of ratio characters. The study of geographic variation, also affected by the latter two difficulties, is particularly important for mygalomorph species, which often exhibit much geographic variation within a relatively small area. Both aims were pursued by an analysis of variation of numerous quantitative and qualitative characters. Initially, variation in a large number of characters was briefly surveyed, and from these the diagnostically most promising were selected and their variation studied in depth.

Variation of quantitative characters (measurements, meristic characters, and ratios formed from these) was analyzed with the aid of a 7094 IBM computer. A Fortran II program directed the computer to calculate the mean and standard deviation of each character for each local population sample of each sex and for certain groupings of local samples plus individual specimens into larger infraspecific or species samples. The computer then compared these samples pairwise in any desired combination, giving for each character for each comparison a value of the distinctness of the two samples. This "distance" value equals the difference between the means of the two samples divided by the sum of their standard deviations. I could then quickly select those quantitative characters of greatest diagnostic value, those showing the most marked geographic variation, and those infraspecific samples that were most divergent.

This analysis of variation was performed on the following number of quantitative characters: 14–15 measurements, 6 meristic characters, and 35 ratios for males; 17 measurements, 9 meristic characters, and 49 ratios for females. These characters were defined so as to be well delimited. Their definitions and abbreviations are as follows (see Figs. 71–75):

CL	Maximum length of carapace (between lines tangent to anteriormost and posteriormost parts of carapace) along line parallel to median longitudinal axis, with lateral border of carapace horizontal.
CW	Maximum width of carapace along line perpendicular to median longitudinal axis.
OQW	Maximum width of eye group (ocular quadrangle) on line perpendicular to median longitudinal axis of carapace. All eye measurements are made in dorsal view with lateral border of carapace horizontal.
ALS	Minimum distance between anterior lateral eyes.
ALD	Maximum diameter of left anterior lateral eye.
AMS	Minimum distance between *pupils* (light colored saucer-shaped central area of eye) of anterior median eyes.
AMD	Transverse diameter of left anterior median eye pupil.
SL	Maximum length of sternum on line parallel to median longitudinal axis. Anterior border of sternum is its pointed anterior extension lateral to labium.
SW	Maximum width of sternum perpendicular to line defining SL.
IFL	Length of femur I taken as length of straight line connecting the proximal and distal points of articulation. All leg and pedipalp segment length measurements were made in side view along retrolateral surface of appendanges after removing them from spider.
ITL	Length of tibia I taken as length of straight line connecting proximal and distal points of articulation.
IML	Length of metatarsus I taken as length

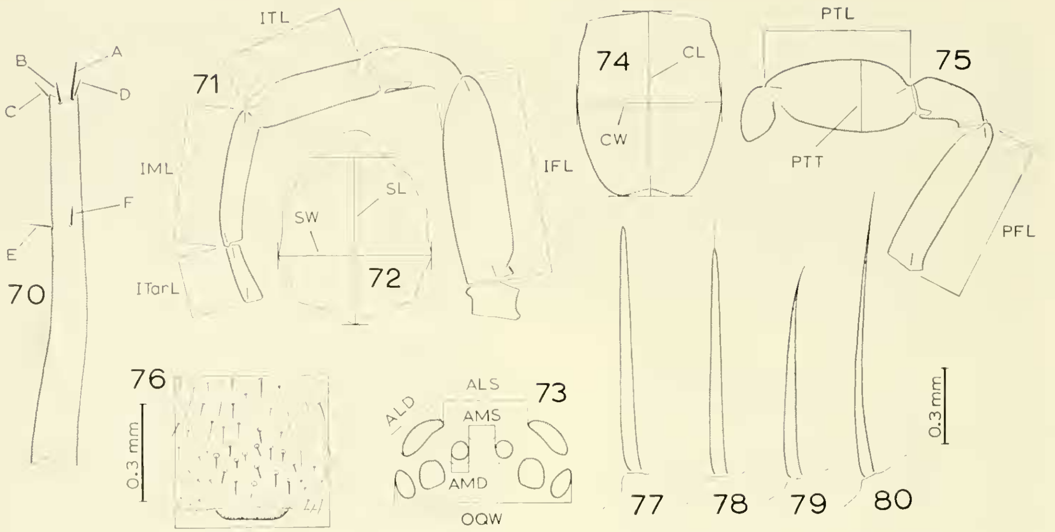


Figure 70. Macrosetae positions on metatarsus I of adult males of *Antrodiaetus*. Figures 71–75. Measurements. Figure 76. Area around genital opening of *Antrodiaetus unicolor*, showing epiandrous gland spigots. 0.3 mm scale. Figures 77–80. Macrosetae types. 77–78. Ensiform. 79–80. Attenuate. 0.3 mm scale.

	of straight line connecting proximal point of articulation with distalmost point of segment.
ITarL	Length of tarsus I taken as length of straight line connecting most proximal exposed point of tarsus with distalmost point of dorsal surface.
IVFL, IVTL, IVML, IVTarL	Leg IV segment lengths measured in same manner as corresponding leg I segments.
ITD, IMD	Diameter of male tibia (metatarsus) I at ventral swelling in lateral view (*A. pugnax* only).
PFL	Length of pedipalpal femur measured same as IFL.
PTL	Length of pedipalpal tibia measured same as ITL.
PTT	Maximum diameter, taken perpendicular to line defining PTL, of pedipalpal tibia in lateral view.
ETL	Distance which tip of inner conductor sclerite extends beyond tip of outer conductor sclerite (*A. unicolor* and *A. robustus* only).
CT	Number of cheliceral macroteeth (per chelicera).
CMT	Number of cheliceral microteeth (per chelicera).
PTSP	Number of ensiform macrosetae on prolateral surface of tarsus of female pedipalp.
PTSR	Number of ensiform macrosetae on retrolateral surface of tarsus of female pedipalp.
IMS	Number of ensiform macrosetae on metatarsus of leg I of female.
IVMT	Number of trichobothria in row on dorsal surface of metatarsus IV. As these usually vary greatly in size, some care must be taken to count small ones also.
IVMCR	Number of setae in large comb on retrolateral surface at distal end of metatarsus IV.
IVCTR	Number of teeth on retrolateral claw of tarsus IV. Claw tooth count includes even the reduced proximal teeth. Counts must be made carefully under high magnification in strong light.
EGS	Number of epiandrous gland spigots. These are located just anterior to genital opening on abdomen of adult males (Fig. 76).

All measurements and counts were performed by myself with the same stereomicroscope and eyepiece micrometer scale. Five specimens were remeasured five times for each character during the course of this study; this sampling indicated that the measurements are accurate to one micrometer unit for each of the four different powers of magnification used. One micrometer unit had the following value for the following characters: 0.0753 mm for CL; 0.0377 mm for CW, SL, SW, and all leg and pedipalp segment lengths; 0.0182 mm for PTT, ITD, and IMD; and 0.0092 mm for all eye group measurements and ETL.

Many of the quantitative characters studied proved to be diagnostically useful. Tables 12–14 record for all species the variation found in the measurements, meristic characters, and diagnostically most valuable ratios. Male measurements of greatest diagnostic value are those of leg I segments, pedipalp segments, and anterior median eye diameter and separation. Ratios formed from these are even more useful. Male leg I macrosetae counts are also particularly useful. Females are much more difficult to diagnose with quantitative characters; ratios are usually much more useful than nonratio characters.

Variation in qualitative characters (those not defined strictly quantitatively) was recorded as carefully as possible and is usually described with the aid of figures. Color variation of *A. unicolor* females was quantified as follows. The color of the lateral slope of the pars cephalica was recorded because of the even coloration, ease of observation, and rather wide range of color variation of this area. All specimens studied had fully sclerotized fangs and had been collected and preserved in 80 per cent ethanol four to six months earlier. The total range of color variation was represented by a rectangular grid (Fig. 92) of 30 squares with the vertical scale representing a basic hue change from yellow to orange and the horizontal (grayness) scale a change in the amount of black in the color. The limits of this range are pale yellow (1A) and dark brown (5.5C). Ten specimens separated by uniform grayness intervals along the A (1A–5A) and C (1C–5C) rows were selected as standards and arranged in a shallow tray of alcohol under the even light of two cool white F15T8-CW fluorescent bulbs. All other specimens were compared individually in the tray with these and each was assigned a value corresponding to its position on the color grid.

The diagnostically most useful male qualitative characters are the shapes and macrosetation of tibia I and metatarsus I, the pedipalpal tibia shape, and the shapes and spatial relationships of the palpus sclerites. Females are considerably more difficult to separate with qualitative characters than are males. Cheliceral and carapace setation, coloration, cheliceral microtooth size and arrangement, and seminal receptacle form are the most useful female characters in species diagnoses.

Species sample sizes are given in Tables 13 and 14, and population sample sizes are indicated in the Dice-Leraas diagrams. Each locality from which a significant sample of *A. unicolor*, *A. pacificus*, or *A. pugnax* was obtained is labeled on the maps of Figures 85, 98, and 104 and identified in the records sections and in the text by an italicized capital letter.

No external structure or characteristic gross change in seminal receptacle form has been found that indicates when a female antrodiaetid has reached sexual maturity (or what instar an adult female may be). Therefore a female specimen was included in a population sample only if it had a longer carapace than the smallest reproductively active female in that sample. Exceptions were made for a few rare species for which no reproductively active females were available. (See species sample sizes given in Table 14.) A reproductively active female is defined as one with large ripening eggs in her abdomen or a brood in her burrow. Other females included in a sample therefore represent first adult instar females collected in the summer, fall, or winter before or soon after their initial mating, some later adult instar females, and occasionally an immature female.

MATERIAL

This study is based upon the following material examined: nearly 370 *Antrodiaetus* males (about 250 are *A. unicolor* and *A. pacificus*), approximately 500 *Antrodiaetus* females (almost 420 are *A. unicolor* and *A. pacificus*), 28 *Aliatypus* males, 55 *Aliatypus* females, and roughly 2000 immature specimens. Approximately half of this material I have collected. The rest was loaned to me by the following people and institutions: Personal collections—J. A. Beatty, J. Carico, P. Craig, H. Exline Frizzell, R. Hoffman, W. Icenogle, R. E. Leech, J. MacMahon, B. J. Marples, F. J. Moore, P. Nelson, W. Peck, V. D. Roth, W. A. Shear, R. Snetzinger, M. Thompson, B. Vogel, A. A. Weaver, T. Yaginuma. Institutions—American Museum of Natural History (W. J. Gertsch); British Columbia Provincial Museum (E. Thorn); British Museum (Nat. Hist.) (J. G. Sheals, D. J. Clark); California Academy of Science; Canadian National Collection (A. L. Turnbull); University of Kansas; Museum of Comparative Zoology (H. W. Levi); University of Nebraska (P. C. Peterson); Muséum National d'Histoire Naturelle, Paris (M. Vachon, M. Hubert); Peabody Museum Natural History, Yale (W. Hartman, C. Remington); and, University of Utah (G. Edmunds).

COLLECTING METHODS

The uncommonness of antrodiaetids in collections is due to their covert behavior. Concentration on particular collecting strategies greatly improves one's chances of finding these spiders. Burrow aggregations are best discovered by locating promising habitats during daylight and searching these habitats for open burrow entrances at night with a headlamp. One can then trap and collect the spiders at their burrow entrances by quickly thrusting a knife blade through the soil and across the burrow lumen just below the spider. More information is gained by excavating the burrow, preferably in daylight after marking it at night. As one accumulates experience, it becomes possible to efficiently locate closed entrances in the daylight by carefully examining and delicately picking at likely microhabitat surfaces with a knife blade. During the mating season, one can (with a headlamp) readily spot adult males as they nocturnally wander over the ground surface in the vicinity of burrow aggregations. Pitfall traps are excellent collectors of wandering males. Careful searching for sealed or nocturnally closed burrow entrances early in the mating season will often reveal penultimate males and recently molted adult males. Penultimate males, easily recognized by their swollen pedipalpal tarsi (Coyle, 1968, fig. 45), will frequently molt to adulthood if maintained in a cool, humid, and dark environment.

MORPHOLOGICAL TERMINOLOGY

Eyes. The abbreviations AME, ALE, PME, and PLE designate the following eyes respectively: anterior median eyes, anterior lateral eyes, posterior median eyes, and posterior lateral eyes.

Chelicerae. A variable prominence, probably homologous to the cheliceral apophysis of *Atypoides*, is found on the anterior-dorsal surface of the chelicerae of *Antrodiaetus* males (Figs. 145–157). This is referred to as the *anterior-dorsal cheliceral prominence.* The *cheliceral macroteeth* are the large teeth forming a single prolateral row (Fig. 158) (and a second more retrolateral row in *Aliatypus*). The *cheliceral microteeth* are the much smaller teeth scattered retrolaterally along part of the prolateral macrotooth row. In the descriptions of microteeth position, the term "last" means most proximal. The presence or absence of a setaless area on the upper ectal (=retrolateral) surface of the chelicera is a useful character in the *unicolor* group of *Antrodiaetus* (Figs. 170–172). The always setaless ectal and dorsal surface proximal of the dorsal gibbosity is *not* part of this character.

Palpus. In *Antrodiaetus,* as in *Atypoides* and *Aliatypus,* the conductor of the palpus consists of two sclerites (Fig. 207), an *inner conductor sclerite* (i.c.s.), which tapers and at least partly envelops the *embolus* distally, and an *outer conductor sclerite* (o.c.s.), which lies outside and cradles these structures.

Male leg I. An *ensiform* macroseta is one which tapers abruptly at its terminal end and is therefore rigid for its entire length (Figs. 77, 78). An *attenuate* macroseta tapers gradually and is therefore very slender distally and often easily bent (Figs. 79, 80). At least 90 per cent of all male tibia I macrosetae can be definitely assigned to one or the other of these two categories. Attenuate macrosetae with broken tips are readily recognized if one is cautious. The macrosetae pattern of male metatarsus I is diagnostically quite useful. Six such differently positioned macrosetae occur in *Antrodiaetus* and are identified by the letters A through F (Fig. 70). When present, each is in nearly the same position in every species and therefore probably homologous throughout the genus, i.e., macroseta A of *A. unicolor* is homologous to that of *A. pugnax,* etc. However, macroseta B shows some position variation, but it seems to vary as much within *A. pugnax* as between other species. In *A. unicolor, A. montanus, A. stygius,* and *A. apachecus* on most male metatarsi I which are recorded as lacking macrosetae in Table 12, macroseta A is represented by a rather prominent enlarged seta.

Abdomen. The abbreviations AL, PM, and PL designate the following spinnerets respectively: anterior lateral, posterior median, and posterior lateral. The anterior half of the abdominal dorsum of *Antrodiaetus* is provided with constantly positioned, segmentally arranged patches of more heavily sclerotized cuticle (Fig. 109), presumably vestigial abdominal tergites. These may be continuous, i.e., fused to one another at adjacent borders. The second patch (from the anterior end), which is always present in both sexes, is smooth, platelike, and most heavily sclerotized; it is called a *tergite* in this paper.

Female genitalia. The general morphology of the female genitalia in *Antrodiaetus* (Fig. 275) is like that of *Atypoides* (see Coyle, 1968).

METHODS OF PRESENTATION

Descriptions. Only the most important literature references are cited. Complete citations are given in Coyle, 1969. Each description is a composite of all adult specimens at hand. Any characters in which the holotype or lectotype is markedly variant are noted. Only characters of diagnostic value are included. The quantitative characters recorded in Tables 12–15 are an integral part of each description. Colors are described from fully sclerotized specimens immersed in ethanol under strong fluorescent light. Only specimens which have been dead in ethanol from six months to five years were used for color descriptions, with a few exceptions as noted.

Diagnosis. The diagnosis lists characters most useful in identifying a given species. These characters are listed in the approximate order of their diagnostic value. Since I often have not repeated characters in the diagnoses of all of several (or a pair of) closely related species, one should examine the diagnoses of all these possibilities when attempting a difficult identification. The absence of female characters with high diagnostic value in many species calls for extreme care when identifying females. It must also be kept in mind, when using a diagnosis based upon a small sample, that the known variation range is probably considerably less than that of the whole species population.

Illustrations. Illustrations were carefully constructed on translucent paper over a squared grid template with the aid of a squared grid reticle in the eyepiece of the stereomicroscope. Figures of female genitalia are always drawn from reproductively active females unless otherwise noted. The thin-walled ducts leading from the seminal receptacle bases to the bursa copulatrix roof are usually incompletely drawn; their openings into the bursa copulatrix are difficult to see under normal illumination.

Records. Unless otherwise noted, only specimens that I have examined are listed in the records section. States and counties (and Japanese prefectures) are given in alphabetical order. Within each county citation, all records from a given locality are separated from those of other localities by a dash. Collection dates are listed only for males. "(♂)" means that the specimen was collected as a penultimate instar on the date indicated and matured later in captivity. When no "♂" or "♀" follows a record, this means that only immatures were collected.

TAXONOMY

ANTRODIAETIDAE Gertsch, 1940

Brachybothriinae Simon, 1892, Histoire Naturelle des Araignées, 1(1): 193. Type genus *Brachybothrium* Simon, 1884 (=*Antrodiaetus* Ausserer, 1871).

Brachybothriidae Pocock, 1903, Proc. Zool. Soc. London, (1): 346.

Acattymidae Kishida, 1930, Lansania, 2(13): 34. Type genus *Acattyma* L. Koch, 1878 (=*Antrodiaetus* Ausserer, 1871).

Antrodiaetinae Gertsch, 1940, *in* Comstock (rev. ed.), The Spider Book, p. 236. Type genus *Antrodiaetus* Ausserer, 1871.

Antrodiaetidae Kaston, 1948, Connecticut Geol. Nat. Hist. Surv. Bull., (70): 48.

Note on family names. Although the name Brachybothriidae is older than either Acattymidae or Antrodiaetidae, Antrodiaetidae has clearly won general acceptance. Antrodiaetidae (and -inae) has been used more frequently (in approximately 17 publications) than either Brachybothriidae (and -inae) (in approximately 14 publications) or Acattymidae (in approximately 7 publications). Antrodiaetidae is the only name used since 1957 (in approximately 14 publications). It is the only name used in works presently reaching a relatively large audience of both professionals and amateurs (Comstock, 1940; Kaston, 1948; Kaston and Kaston, 1953; Yaginuma, 1960; Kaestner, 1968; Levi and Levi, 1968), with the exception of Gertsch's (1949) use of Acattymidae. In accordance with Article 40 of the recent (1961) International Code of Zoological Nomenclature, both the present general acceptance of the name Antrodiaetidae and the replacement before 1961 of the two older names by Antrodiaetidae because of the synonymy of their type genera with the senior synonym *Antrodiaetus* (Kaston, 1948; Yaginuma, 1962) clearly justify rejection of the older names and adoption of Antrodiaetidae.

Characteristics. Carapace: Pars cephalica elevated above pars thoracica. Eyes grouped on a median prominence. ALE's largest; form a slightly procurved transverse row with AME's. PLE's form lateral limits of eye group. PME's widely separated; close to respective PLE's. *Sternum:* Four pairs of sigilla; anterior pair large, just behind labium and sometimes indistinct; posterior pair larger than second or third pairs. Labium well defined but fused to sternum; inclined from plane of sternum. *Chelicerae:* Female chelicerae very robust; strongly gibbous dorsally. Rastellum well developed on females. One row of macroteeth on prolateral side of closed fang; sometimes a macrotooth row also on retrolateral side of closed fang. Microteeth on retrolateral side of prolateral macrotooth row. *Pedipalps:* Coxal endite very small. Female tarsus with 2 rows of macrosetae (on prolateral and retrolateral aspects of ventral surface). Male tibia swollen. Palpus with well defined o.c.s., i.c.s., and embolus. I.c.s. at least partly envelops embolus distally. *Legs:* Female legs relatively stout and with many macrosetae. *Abdomen:* Males with 1 to 4 segmentally arranged (sometimes fused) sclerotized patches dorsally; second patch most heavily sclerotized, tergitelike, and always present. Females possess only this second tergite; rarely other patches also. Epiandrous gland spigots clustered just anterior to male genital opening. AL spinnerets 2-segmented and functional; reduced and unsegmented; or absent. PM's unsegmented and functional. PL's 3-segmented and functional; distal segment length not over $1\frac{1}{2}$ that of middle segment. *Female genitalia:* Genital opening broad slit shared by uterus exit; not markedly sclerotized externally. Four seminal receptacles with stalk and apical enlarged portion open into chamber (bursa copulatrix) just inside genital opening.

Diagnosis. Males of this family can be separated from those of the Mecicobothriidae and Atypidae by the possession of a strongly sclerotized i.c.s. which is distinct from the o.c.s.; or, if the i.c.s. is not strongly sclerotized, then by the possession of either only two pairs of spinnerets or a pedipalpal patella almost as long as the tibia. Antrodiaetid females can be distinguished from both mecicobothriid and atypid females by the presence of a rastellum, from the former group by the strongly elevated pars cephalica and a proportionately much shorter distal PL spinneret segment, and from atypids by the two rows of pedipalpal tarsus macrosetae.

Provisional inclusion of Aliatypus. As is emphasized in the discussion of phylogeny, *Antrodiaetus* and *Atypoides* form a monophyletic group distinct from *Aliatypus.* A number of character states which these two distinct groups share could be the result of convergence or at least parallel evolution rather than indicators of recent common ancestry. In heavily weighted genitalia characters, *Aliatypus* strongly resembles the family Mecicobothriidae; it is possible that *Aliatypus* is more closely related to this family than to *Antrodiaetus* and *Atypoides.* Perhaps *Aliatypus* will prove sufficiently distinct phylogenetically and ecologically to merit consideration as a separate family. (The resulting four small relict atypoid taxa [Liphistiidae not included] might for convenience's sake be reduced to subfamilies under a single family name.) Only after close study of *Aliatypus* and the mecicobothriids can the approximate phylogenetic position and proper classification of *Aliatypus* be resolved. I shall provisionally retain *Aliatypus* within the family Antrodiaetidae.

KEY TO GENERA OF ANTRODIAETIDAE

1a. Thoracic groove longitudinal. AL spinnerets absent (Fig. 318) or unsegmented with at most one spigot apically. No cheliceral macroteeth on retrolateral side of closed fang (Fig. 158). Female IVMT = 5–21. Male pedipalpal patella much shorter than tibia (Figs. 173–187). Burrow entrance a collar or turret (Figs. 12, 26, 32) 2

1b. Thoracic groove an irregular deep pit, a shallow rounded depression, or absent. AL spinnerets 2-segmented (may be indistinctly segmented) with at least several spigots clustered apically (Fig. 328). Female with small row of cheliceral macroteeth on retrolateral side of closed fang (Fig. 322). Female IVMT = 1–4 (rarely more than 1). Male pedipalpal patella nearly as long as tibia (Fig. 324). Burrow entrance a trapdoor (Fig. 39) .... *Aliatypus*

2a. 2 pairs of spinnerets (AL's absent) (Fig. 318). Male without cheliceral apophysis. (Do not mistake anterior-dorsal prominence for apophysis.) (Figs. 145–157) .... *Antrodiaetus*

2b. 3 pairs of spinnerets (AL's present; may be extremely reduced in some specimens of *A. gertschi.*). Adult male with cheliceral apophysis .... *Atypoides*

Antrodiaetus Ausserer, 1871

Antrodiaetus Ausserer, 1871, Verh. zool.-bot. Ges. Wien, 21: 136. Type species by monotypy *Mygale unicolor* Hentz (See *Antrodiaetus unicolor* description for discussion of identity of this species.). –Bonnet, 1955, Bibliographia Araneorum, 2: 335.

Acattyma L. Koch, 1877, Verh. zool.-bot. Ges. Wien, 27: 760. Type species by monotypy *Acattyma roretzi* L. Koch. –Bonnet, 1955, Bibliographia Araneorum, 2: 141.

Brachybothrium Simon, 1884, Bull. Soc. Zool. France, 9: 314. Type species by subsequent designation (Simon, 1892) *Brachybothrium pacificum* Simon. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Nidivalvata Atkinson, 1886, Ent. Amer., 2: 129. Type species here designated *Nidivalvata marxii* Atkinson.
Anthrodiaetus: Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 312.

Notes on synonymies. Simon (1890) first synonymized *Nidivalvata* and *Brachybothrium.* Although he later (1892) suggested that *Antrodiaetus* and *Brachybothrium* might be synonymous, such a synonymy was not designated until 1930 by Kishida and later by Gertsch and Jellison (1939) before receiving general acceptance. Both Pocock (1903) and Simon (1903) first suggested that *Acattyma* and *Brachybothrium* might be synonymous, but this synonymy was not proposed until 1960 by Yaginuma (see also Yaginuma, 1957). As I stress in the discussion of antrodiaetid phylogeny, *Antrodiaetus roretzi* (type species of Koch's monotypic genus *Acattyma*) is an evolutionary relict distinct from, but clearly related to, other species of *Antrodiaetus* and *Atypoides.* Its distinctness may justify re-establishment of the monotypic genus, but until it is more thoroughly studied, I believe it advantageous to retain it within *Antrodiaetus.*

Descriptive diagnosis. Carapace: Thoracic groove longitudinal. *Sternum*: Labium slightly to moderately inclined from plane of sternum. *Chelicerae*: Female with single row of 8 to 17 macroteeth along prolateral side of closed fang; microteeth along posterior portion of and retrolateral to this macrotooth row. Larger microteeth predominantly in retrolateral portion of microtooth group. Male with anterior dorsal prominence of varying size. *Pedipalps:* Male patella much shorter than tibia; tibia swollen, elongate to short and thick. O.c.s. of palpus tapers distally or very wide (*A. roretzi*). I.c.s. clearly separate from o.c.s. distally. *Legs:* 5 to 21 trichobothria dorsally on female metatarsus IV. Zero to 6 teeth on each of prolateral and retrolateral claws of female tarsus IV. Male tibia I with prolateral group of macrosetae or enlarged setae; metatarsus I without macrosetae or with one to few macrosetae distal of midpoint. *Spinnerets:* Only 2 pairs (PM, PL); both functional. *Genitalia:* Seminal receptacle stalks not sinuous; stalk and bowl markedly more sclerotized than bulb. *Behavior:* Burrow entrance a collapsible collar.

Misplaced species. Accatima cunicularia Simon, *Accatima davidi* Simon, and *Acattyma cryptica* Simon, all Ctenizidae, were incorrectly placed in the genus *Acattyma* L. Koch (Simon, 1886, 1892, 1897). Pocock (1901) recognized this error and listed diagnostic features of *Acattyma* L. Koch after describing a new ctenizid genus, *Latouchia*, which he felt was equivalent to *Acattyma* Simon. Simon (1903) later acknowledged his error and placed the three species in *Latouchia.* Crome (1955) describes and illustrates the abdominal anatomy of an "*Acattyma* spec.," but the very short 2-segmented PL spinnerets show that this is not an antrodiaetid.

Species groups and key. Antrodiaetus consists of three monophyletic species groups: the *unicolor* group (9 species), the *lincolnianus* group (3 species), and the *roretzi* group (1 species). The following key first separates the species groups and then the species of each group. The males of each of these taxa are morphologically more distinct than the females and can be much more quickly and confidently identified. *A. occultus* females are unknown but will likely key out to *A. pacificus.*

KEY TO SPECIES OF *ANTRODIAETUS*

Males

1a. O.c.s. of palpus very broad distally (Fig. 233). Prominent tibia I prolateral macrosetae group centered just proximal of midpoint; these macrosetae erect and quite elongate (Fig. 268). Japan (island of Honshu) .... (*roretzi* group) *roretzi*

1b. O.c.s. much narrower distally (Figs. 188–232). Tibia I prolateral macrosetae group, if prominent, centered at or distal of midpoint (Figs. 234–267). N. America or Japan (island of Hokkaido) 2

2a. Relatively inconspicuous group of enlarged setae on prolateral surface of tibia I (Figs. 262–267). Pedipalpal tibia relatively slender (PTT/PTL = 0.23–0.34); greatest diameter in lateral view distal of midpoint (Figs. 184–186) .... (*lincolnianus* group) 3

2b. Prominent tibia I prolateral macrosetae group (Figs. 234–261). Pedipalpal tibia more swollen (PTT/PTL = 0.33–0.54); greatest diameter in lateral view proximal of midpoint (Figs. 173–183) .... (*unicolor* group) 5

3a. Tips of i.c.s. and o.c.s. of palpus about even and very weakly sclerotized; sperm reservoir looped loosely (Figs. 224, 225). Pedipalpal tibia very elongate (PTT/PTL =0.23–0.25) (Fig. 184). AME very small (AMD/AMS = 0.27–0.37) (Fig. 127). Abdomen dark. Central U. S. (Nebraska, Kansas) .... *lincolnianus*

3b. Tip of i.c.s. extends well beyond o.c.s. tip; both well sclerotized; sperm reservoir looped tightly (Figs. 226–232). Pedipalpal tibia not as elongate (PTT/PTL = 0.29–0.34) (Figs. 185, 186). AME not as small (AMD/AMS = 0.36–0.78) (Fig. 128). Abdomen paler yellow-gray. Central or southwestern U. S. 4

4a. O.c.s. tip thin, spatulate, bent away from i.c.s. (Figs. 226–228). IFL/ITarL =2.12–2.29. Central U. S. (Arkansas, Missouri) .... *stygius*

4b. O.c.s. tip moderately thickened and erect (Figs. 229–232). IFL/ITarL = 2.29–2.54. Southwestern U. S. (Arizona, New Mexico) .... *apachecus*

5a. Eastern U. S. (east of Great Plains) 6

5b. Western N. America (Rocky Mtns. or westward) or Japan 7

6a. More than 20 per cent of macrosetae in tibia I prolateral macrosetae group are ensiform (Figs. 234–240). Metatarsus I macroseta B almost never present. Distalmost macroseta on retrolateral aspect of ventral surface of tibia I almost always less than 3/4 of distance from proximal to distal end (Figs. 234–240) .... *unicolor*

6b. Less than 20 per cent of macrosetae in tibia I prolateral macrosetae group are ensiform (Fig. 241). Metatarsus I macroseta B usually present (Fig. 243). Distalmost macroseta on retrolateral aspect of ventral surface of tibia I 3/4 or more of distance from proximal to distal end (Fig. 241) .... *robustus*

7a. Less than 30 per cent of macrosetae in tibia I prolateral macrosetae group are ensiform (Figs. 244–247). ITL/IML= 0.65–0.81. O.c.s. tip closely appressed to i.c.s. (Figs. 197–203) .... *pacificus*

7b. More than 30 per cent of macrosetae in tibia I prolateral macrosetae group are ensiform (Figs. 248–263). ITL/IML = 0.81–0.99. O.c.s. tip may or may not be closely appressed to i.c.s. (Figs. 204–225) 8

8a. Metatarsus I with strong retrolaterally and ventrally produced "elbow" just proximal of midpoint, *and* macrosetae group on distal half of ventral aspect of retrolateral surface of tibia I (Figs. 256, 257) .... *hageni*

8b. Metatarsus I lacking such a protuberance (Figs. 258–261); *or* protuberance keellike and macrosetae group on retrolateral aspect of ventral surface of tibia I proximal of distal 1/3 of segment (Figs. 250–252, 101) 9

9a. Tibia I and metatarsus I shapes and macrosetation similar to Figs. 258, 259. ITL/ITarL = 1.64–1.66. AME small (AMD/CL = 0.016–0.018) (Fig. 126). Side of i.c.s. against o.c.s. translucent (Fig. 220) .... *cerberus*

9b. Tibia I and metatarsus I not as above. ITL/ITarL = 1.31–1.64. AME larger (AMD/CL = 0.020–0.033). I.c.s. not partly translucent (Fig. 213) 10

10a. ITL/IML greater than 0.93. Tibia and metatarsus I shapes and macrosetation similar to Figs. 260, 261. Japan (island of Hokkaido) .... *yesoensis*

10b. ITL/IML less than 0.93. Tibia I and metatarsus I not as above. Western N. America 11

11a. Tibia I and metatarsus I with ventral swellings of varying prominence (Figs. 250–252, 101); small group of large macrosetae positioned on tibia I ventral swelling. Metatarsal macroseta A always present .... *pugnax*

11b. Tibia I and metatarsus I shapes and macrosetation not as above 12

12a. Pedipalpal tibia strongly swollen (PTT/PTL = 0.44–0.49) (Fig. 178). ITL/CL = 0.57–0.63. Tibia I and metatarsus I shapes and macrosetation similar to Figs. 248, 249. Large setaless area on upper ectal cheliceral surface .... *occultus*

12b. Pedipalpal tibia not as swollen (PTT/PTL = 0.35–0.41) (Fig. 180). ITL/CL = 0.66–0.77. Tibia I and metatarsus I shapes and macrosetation similar to Figs. 253–255. Setae distributed over entire upper ectal cheliceral surface (Fig. 150) .... *montanus*

Females

1a. Bursa copulatrix distinctly divided into 2 lateral pouches by a median partition (Figs. 310–312). Seminal receptacles closely paired, stalks long and slender, bowls weakly developed. Setae absent (or very rare) on labium except for anterior and lateral edges. Japan (island of Honshu) .... (*roretzi* group) *roretzi*

1b. Bursa copulatrix without median partition. Seminal receptacles not or only weakly paired, *or* stalks short to moderately long, *or* bowls moderately to strongly developed (Figs. 270–309). (Some eastern *A. pacificus* individuals are exceptions.) Setae scattered over much of labium. N. America or Japan (island of Hokkaido) 2

2a. From southwestern U. S. (Arizona, New Mexico) or central U. S. (Arkansas, Missouri, Kansas, Nebraska). If from central U. S. then AMD = 0.09–0.13 mm (Figs. 135, 136). IVCTR usually 0 to 2, cheliceral microteeth proportionately large (Figs. 166, 167) .... (*lincolnianus* group) 3

2b. Elsewhere or if from central U. S. (*A. unicolor*) then AMD = 0.11–0.22 mm (Fig. 130), IVCTR usually 3 or more, cheliceral microteeth proportionately smaller (Fig. 158) .... (*unicolor* group) 5

3a. Stalk and bowl portion of seminal receptacles weakly sclerotized and small, border with bulb poorly defined (Figs. 304, 305). Abdomen rather dark yellow-gray or medium brown. CMT/IVMT greater than 2.50. Central U. S. (Nebraska, Kansas) .... *lincolnianus*

3b. Stalk and bowl portion well sclerotized and slightly larger, border with bulb well defined (Figs. 306–309). Abdomen lighter. CMT/IVMT = 1.00–2.25. Southwestern or central U. S. 4

4a. IVML/IML = 1.36–1.38. IFL/IVFL = 1.04–1.05. Carapace narrower (CW/CL = 0.76–0.77) (Fig. 118). Central U. S. (Arkansas, Missouri) .... *stygius*

4b. IVML/IML = 1.21–1.26. IFL/IVFL = 1.09–1.13. Carapace broader (CW/CL = 0.78–0.82). Southwestern U. S. (Arizona, New Mexico) .... *apachecus*

5a. Japan (island of Hokkaido) .... *yesoensis*

5b. North America 6

6a. Eastern U. S. (east of Great Plains) 7

6b. Western N. America (Rocky Mtns. and westward) 8

7a. Combined presence of minute AL spinneret vestiges (Fig. 317), rather short densely distributed dorsal abdominal background setae (Fig. 316), *and* thin elongate setae dorsally just posterior of pedicel (Fig. 314). Seminal receptacle stalks not expanded basally (Figs. 280–283). SL/SW = 1.08–1.16 .... *robustus*

7b. Lacking one or more of first 3 character states above; usually no AL spinneret vestiges, usually longer more sparsely distributed dorsal abdominal background setae (Fig. 315), usually shorter thicker setae dorsally just posterior of pedicel (Fig. 313). Seminal receptacle stalks usually expanded basally (Figs. 270–279). SL/SW = 1.13–1.27 .... *unicolor*

8a. Setae distributed over entire upper ectal surface of chelicera (Figs. 171, 172). Carapace pale to medium dark gray-yellow 9

8b. Small to large setaless area on upper ectal surface of chelicera (Fig. 170). Carapace usually darker 11

9a. CL over 6.2 mm, IFL/IML less than 1.69, posterior abdominal dorsum without darkly pigmented area, IVTL/CL = 0.40 or more, *and* seminal receptacles unpaired (Figs. 292–302) 10

9b. CL under 6.2 mm or IFL/IML = 1.69 or more *or* abdominal dorsum dark *or* IVTL/CL = 0.41 or less *or* seminal receptacles paired (Figs. 288–291) 11

10a. Seminal receptacle stalks not expanded basally (Figs. 299–300). SL/SW=1.20–1.37 (Fig. 141) .... *hageni*

10b. Seminal receptacle stalks expanded basally (Figs. 295–298). SL/SW = 1.06–1.19 (Fig. 140) .... *montanus*

11a. IVTL/IVTarL = 1.90 or more. IVML/IML = 1.42 or more .... *cerberus*

11b. IVTL/IVTarL less than 1.90. IVML/IML = 1.09–1.50 12

12a. ITarL usually more than 1.28 mm. IVML/IML = 1.09–1.38 .... *pacificus*

12b. ITarL usually less than 1.28 mm. IVML/IML = 1.31–1.50 .... *pugnax*

THE *UNICOLOR* GROUP

Descriptive diagnosis. Male: AMD usually proportionately medium to large; AME's narrowly to widely separated (AMD/AMS, AMD/CL; Table 13). Setae scattered over much of labium; setaless area just posterior of labium relatively small. Pedipalpal tibia moderately to strongly swollen (PTT/PTL, Table 13); greatest diameter in lateral view proximal of midpoint. O.c.s. of palpus heavily sclerotized; surface very rough (filelike); relatively narrow apically. Group of strong macrosetae on prolateral surface of tibia I centered at or distal of midpoint; macrosetae also scattered or clustered on retrolateral aspect of ventral surface of tibia I

(Table 12). *Female:* Carapace relatively narrow to moderately broad (CW/CL, Table 14). Labium setation as in male. Cheliceral microteeth proportionately small to large; few to many (CMT, Table 14). Tarsus IV claws (both prolateral and retrolateral) usually with 3 or more teeth (IVCTR, Table 14). Leg IV segments usually proportionately long (IVML/CL, Table 14). Bursa copulatrix lacks median partition. Seminal receptacles medium to large in proportion to body size, stalk generally of moderate length, bowl usually well developed, and receptacles usually not closely paired.

Antrodiaetus unicolor (Hentz)

Figures 113, 120, 130, 138, 145–146, 158, 173–174, 188–194, 234–240, 270–279, 313, 315, 318. Map 1.

Mygale unicolor Hentz, 1841, Proc. Boston Soc. Nat. Hist., 1: 42. Holotype female from Alabama; destroyed. –, 1842, Jour. Boston Soc. Nat. Hist., 4: 57, pl. 7, fig. 5.

Mygale gracilis Hentz, 1841, Proc. Boston Soc. Nat. Hist., 1: 42. Holotype male from Alabama; destroyed. NEW SYNONYMY. –, 1842, Jour. Boston Soc. Nat. Hist., 4: 56, pl. 7, fig. 4.

Antrodiaetus unicolor: Ausserer, 1871, Verh. zool.-bot. Ges. Wien, 21: 136. –Roewer, 1942, Katalog der Araneae, 1: 189. –Bonnet, 1955, Bibliographia Araneorum, 2: 335.

Closterochilus gracilis: Ausserer, 1871, Verh. zool.-bot. Ges. Wien, 21: 142. –Roewer, 1942, Katalog der Araneae, 1: 190.

Eurypelma bicolor: Marx, 1883, *in* Howard (ed.), Invertebrate Fauna of South Carolina, p. 24.

Eurypelma gracilis: Marx, 1883, *in* Howard (ed.), Invertebrate Fauna of South Carolina, p. 24.

Brachybothrium accentuatum Simon, 1884, Bull. Soc. Zool. France, 9: 315. Holotype an immature female from North Carolina; in the Muséum National d'Histoire Naturelle in Paris; examined. NEW SNYONYMY. –Roewer, 1942, Katalog der Araneae, 1: 189. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Nidivalvata marxii Atkinson, 1886, Ent. Amer., 2: 130, 110, 111, 113, 116, 131, pl. 5, figs. 8–10, 13, 17, 18, 23. Holotype female (immature ?) from North Carolina, probably Chapel Hill; either in the U. S. National Museum or in the Cornell University collection (see comment below); "Type" from Cornell examined. NEW SYNONYMY.

Nidivalvata angustata Atkinson, 1886, Ent. Amer., 2: 130, 113, 117. Two female syntypes from North Carolina, probably Chapel Hill; in the U. S. National Museum and/or the Cornell University collection (see comment below); "Type" from Cornell examined. NEW SYNONYMY.

Brachybothrium marxi: Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 310. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Brachybothrium angustatum: Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 310. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Anthrodiaetus unicolor: Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 312.

Brachybothrium pacificum: Barrows (not Simon, 1884), 1918, Ohio Jour. Sci., 18(8): 298. –Barrows, 1925, Ann. Ent. Soc. America, 18(4): 493, pl. 37, figs. 17–22.

Missulena gracilis: Petrunkevitch, 1939, Trans. Connecticut Acad. Arts Sci., 33: 213. –Bonnet, 1957, Bibliographia Araneorum, 2: 2939.

Antrodiaetus bicolor: Vogel, 1962, Ent. News, 73 (9): 246.

Comments on synonymy and descriptions. Hentz's (1841, 1842) poor descriptions have caused much uncertainty and some confusion concerning the placement of his two species (Ausserer, 1871; Marx, 1883; Simon, 1892; Petrunkevitch, 1911b and 1939). Unfortunately, no one redescribed Hentz's type specimens before their destruction. (Apparently the types were part of a pinned collection housed by the Boston Society of Natural History and destroyed by insects [H. W. Levi, personal communication].) Simon (1892) first indicated that *Mygale unicolor* might be similar to species of *Brachybothrium*, but not until Gertsch and Jellison's (1939) brief statement have authors generally acknowledged this similarity. Although Simon (1892) also indicated the similarity of *Mygale gracilis* to *Brachybothrium* species, no author has subsequently expressed this opinion.

Hentz describes or illustrates sufficient diagnostic characters to show that *Mygale gracilis* belongs to the taxon *Antrodiaetus* as presently defined. In addition to an antrodiaetid body form, eye arrangement, and pedipalp shape, a conductor is illustrated on the palpus, the spinnerets are long, and metatarsus I is sinuous. (Hentz presumably misinterpreted this curvature as a "notch.") Unfortunately the identity of *Mygale unicolor* is less certain. The eye arrangement is strange, no thoracic groove is illustrated, and spinneret form is not mentioned. The reduced endites and general body form are antrodiaetidlike. To avoid upsetting the generic and familial nomenclature, I have decided that—as the meager evidence in Hentz's descriptions indicates—these two names are synonymous, and as first reviser I select *Mygale unicolor* as the senior synonym.

Atkinson (1886) did not indicate the type deposition of the two species he described. Simon (1890), who was loaned the type of *Nidivalvata marxi*, reported that the Atkinson types were in the U. S. National Museum. However, a small adult female labeled "Type *Brachybothrium angustata*" and a probably immature female labeled "Type *Brachybothrium marxii*" are in the Cornell University collection presently housed in the AMNH. Unfortunately the USNM "types" are presently unavailable for study. The Cornell specimens do not match the carapace dimensions recorded by Atkinson for the specimens he described. Although unable to examine the syntypes of *Nidivalvata angustatum*, Simon (1890) stated that this was perhaps a synonym of *Brachybothrium accentuatum*. He examined the type of *N. marxi* and noted its great similarity to *B. accentuatum*. He described the pedipalpal tarsus as being swollen (an indication that the specimen may be a penultimate male), using this as the diagnostic character of *B. marxi* in a key to species.

Description. See Tables 12–14, which contain measurements, meristic data, and diagnostic ratios for a sample of the species.

Male. Carapace: Figure 120. Setae very sparse on pars thoracica, sometimes moderately dense along lateral border. *Chelicerae:* Figures 145, 146. Large setaless area on upper ectal surface. *Pedipalps:* Figures 173–174, 188–194, 81. Tibia moderately to strongly swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus usually blunt (occasionally rather pointed); closely appressed to i.c.s. I.c.s. tip well sclerotized; often slightly curved; usually tapered to relatively narrow point. *Leg I:* Figures 234–240. Group of macrosetae (33% to 100% are ensiform) centered at 1/2 to 2/3 of distance from proximal to distal end of tibia on prolateral surface. Fewer more scattered macrosetae (0% to 100% are ensiform) along retrolateral aspect of ventral surface of tibia; distalmost macroseta of this group positioned at 2/3 or less (rarely at 3/4) of distance from proximal to distal end. Zero to 8 macrosetae (0% to 100% are ensiform) scattered between these groups, mainly along prolateral aspect of ventral surface. Tibia nearly cylindrical except sometimes swollen at prolateral macrosetae group. One to 3 (rarely none) macrosetae ventrally at distal end of metatarsus; rarely a macroseta present at 2/3 of distance from proximal to distal end on prolateral surface. Metatarsus weakly to moderately sinuous in ventral view. *Abdomen:* 3 dorsal heavily sclerotized usually continuous patches. Posterior patch smaller than anterior 2; occasionally reduced to bilateral pair of sclerotized spots. *Coloration:* Carapace pale gray-yellow to brown. Sternum pale yellow to gray-yellow; pedipalpal coxae similar to or slightly darker than sternum; labium markedly darker than sternum. Patella, tibia, and metatarsus of leg I light gray-orange to dark red-brown, usually darker than carapace; femur dorsally slightly lighter than more distal segments, ventrally even lighter. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray to gray-brown or purple-gray; dorsal sclerotized patches slightly darker except sclerite of second patch usually similar to carapace.

Female. Carapace: Figure 130. Setae sparse to moderately dense on pars thoracica; densest along lateral border. *Sternum:* Figure 138. *Chelicerae:* Figure 158. Microteeth positioned beside last 9 to last 3 macroteeth; frequently extend beyond last macrotooth. Microteeth usually proportionately small to medium size. Large setaless area on upper ectal surface. *Abdomen:* Figures 313, 315. Dorsal background setae sparsely to moderately long. Convergent median dorsal setae just posterior to pedicel usually short and rather stout; occasionally long and slender. *Genitalia:* Figures 270–279. Seminal receptacles with well-sclerotized stalk and bowl; vary from moderately long and moderately thick to quite stout. Stalk usually expanded (sometimes slightly) at base. Bowl well developed; its border with bulb sharply defined. Floor of bursa copulatrix weakly sclerotized. *Coloration:* Carapace pale yellow to dark brown; pars cephalica usually darker than pars thoracica. Sternum similar to pars thoracica; labium much darker. often similar to chelicerae; pedipalpal coxae usually slightly lighter than labium. Chelicerae pale gray-yellow to dark red-brown, usually darker than pars cephalica. Pedipalps and legs dorsally similar to adjacent portion of carapace, ventrally lighter. Abdomen pale yellow-gray to dark brown, sometimes with faint chevron pattern dorsally behind tergite; tergite usually similar to pars thoracica.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 234–240; Table 12) are distinctive for this species and include the best diagnostic characters. *A. unicolor* has a proportionately long metatarsus I (Fig. 235), a proportionately short pedipalpal femur, and relatively large AME's (Fig. 120) so that ITL/IML, PFL/CL, and AMD/CL (Table 13) are sometimes useful in distinguishing this species from other *unicolor* group species. *Females.* Characters useful in separating *A. unicolor* females from those of the sympatric *A. robustus* are listed in the *A. robustus* diagnosis. If *A. unicolor* were not geographically separated from the other *unicolor* group species, identification of females would be difficult or impossible. Because of a proportionately short femur I and a fairly small mean CMT number, *A. unicolor* females differ most from *A. pacificus* and *A. cerberus* females in IFL/CL and some other IFL ratios (Table 14) and from *A. pacificus* and *A. montanus* in CMT number (Table 14).

Variation. Males. Although most characters studied exhibit large variation, only a small number of these vary discontinuously. Strong geographic variation occurs with the following ratios (listed in order of degree of discontinuous variation): PTT/PTL (Fig. 81), IML/ITarL (Fig. 83), IML/CL (Fig. 82), ETL/CL (Fig. 84), PFL/CL, ALD/CL, and ITL/IML. In these, all samples (*B, C, E, F, G, I, P, Q*) (Fig. 85) except two (*A, N*) are connected to others by broadly overlapping variation ranges. Sample *A*, clearly the most divergent sample, is particularly divergent in ratios IML/CL (Fig. 82), ETL/CL (Figs. 84, 188–194), PFL/CL, and PTT/PTL. Sample *N* is also divergent, especially in PTT/PTL (Figs. 81, 174), IML/ITarL (Fig. 83), and IFL ITarL. Sample *A* is much more similar to *N* in most characters with strong geographic variation than to other samples, whereas *N* is usually only slightly more similar to *A* than to other samples. Individuals of both samples usually have a more swollen pedipalpal tibia and a proportionately shorter metatarsus I and pedipalpal femur than other males. Sample *A* individuals have a particularly small ETL. Sample *N* males have a proportionately long tarsus I.

ITL, IML, PTL, and PFL have the least continuous geographic variation of any measurements, but other measurements correlated with body size show similar patterns of weaker geographic variation in which the small-bodied sample *A* is somewhat divergent and the slightly larger-bodied males from *N* are less divergent from the rest of the samples (Figs. 81, 82). Among meristic characters the strongest geographic variation occurs in the number of prolateral tibia I ensiform macrosetae (Figs. 87, 234–240). Sample *N*, with few such macrosetae, is divergent, but its variation overlaps that of other samples. Sample *Q* and several males at *E* possess a distinctly higher number of ensiform macrosetae on the prolateral aspect of the ventral surface of tibia I (Fig. 240) than do most other *A. unicolor* males. Male carapace color varies in a geographic pattern similar to that in the females (see below), but the variation is continuous.

The single male from *O* is particularly divergent in two characters; the pedipalpal tibia is strongly swollen like that of males at *A* and *N* (Fig. 81), and metatarsal I macrosetae are absent (Table 12). The single male from *L* is extremely small (Fig. 82) but in all ratios and other nonmeasurement characters closely resembles most males (except those from *A* and *N*).

Noteworthy continuous variation occurs in several characters. The o.c.s. tip, usually blunt and rounded (Figs. 189, 191), is rarely almost pointed (Fig. 194). Extremely wide variation occurs in EGS number (Fig. 86), which is correlated with body size. The relative size and shape of the anterior-dorsal cheliceral prominence varies considerably. Figure 146 illustrates an exceptionally small prominence, Figure 145 a slightly larger than normal prominance. The metatarsus I macrosetae pattern also varies widely (Figs. 234, 236; Table 12).

Females. Strong geographic variation occurs in five ratio characters (listed in order of approximate degree of discontinuity): IFL/IVFL (Fig. 88), IVML/CL, IVTL/CL (Fig. 93), ALS/CL, and IVML/IML (Fig. 89). Samples *I* and *D* are each divergent from many other samples in some of these characters. No measurements or meristic characters exhibit strong geographic variation.

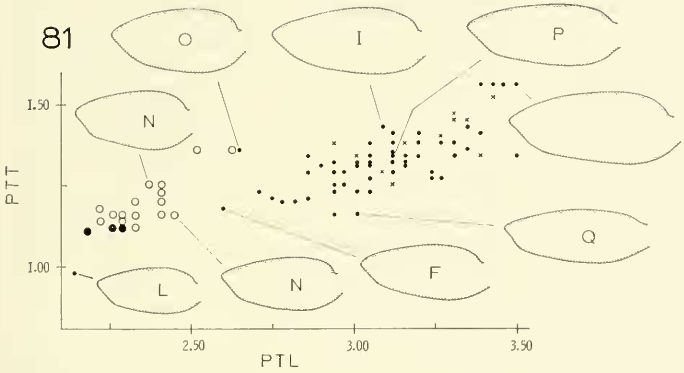
Unlike the males, in which each population sample is homogeneous, some female samples show discontinuous variation within. One of the strongest and, to the casual observer, most obvious instances of discontinuous variation in this species is in coloration, particularly female carapace coloration (Fig. 92). Most samples are homogeneously either light or dark with little overlap between these light and dark samples. In a few localities (*I, K, L*), however, distinct light and dark individuals were found living sympatrically. Although light populations appear to be more common in the south and west part of the species range, dark females have been collected in the western parts of Tennessee and Kentucky and in Arkansas.

An extensive search was made for characters (other than color) which might also distinguish dark and light samples. Several ratio characters separated light and dark specimens in each of samples *I, K,* and *L*, but only SW/SL exhibits such nearly discontinuous variation in all three samples.

→

Figures 81–87. Geographic variation in *Antrodiaetus unicolor* males. (All measurements in mm. For scatter diagrams, large black dots represent sample A, circles sample N, and small black dots rest of species sample.) 81. Scatter diagram of PTT and PTL; representative specimens illustrated. (X's represent *Antrodiaetus robustus* males.) 82. Scatter diagram of IML and CL. 83. Scatter diagram of IML and ITarL. 84. Modified Dice-Leraas diagram of ETL/CL variation compared with that of *A. robustus*. (Horizontal line represents the observed range, vertical line the mean, open rectangle the standard deviation, solid black rectangle the 95 per cent confidence interval for the mean, number to right of range line the sample size, and letter in left column the sample locality.) 85. Map of population sample localities. 86. Histogram of EGS number compared with that of *A. robustus*. (One unit of vertical scale represents one specimen.) 87. Histogram of number of ensiform macrosetae on prolateral surface of tibia I. (One unit of vertical scale represents one tibia.) Right column contains percentage of ensiform macrosetae out of total number of macrosetae in this group.

81



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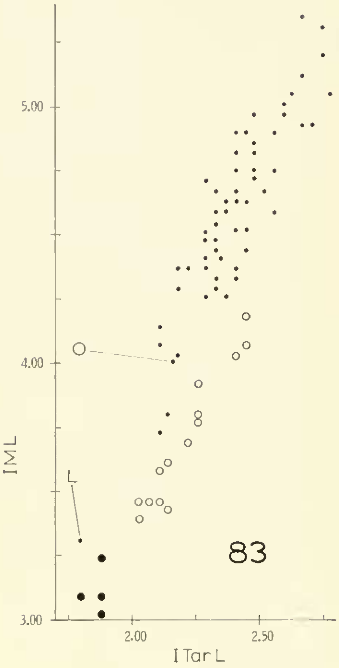

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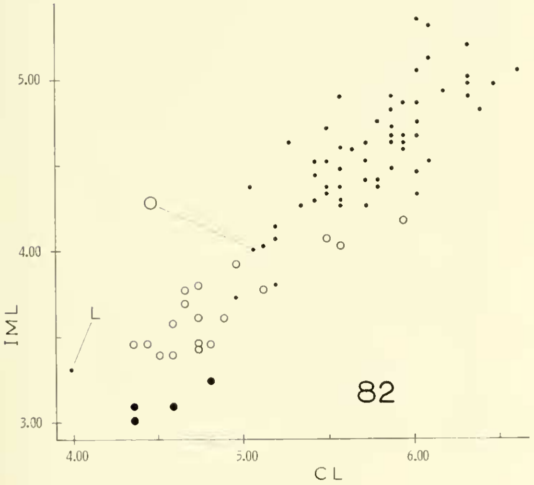

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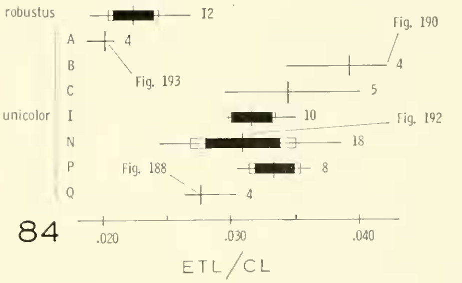

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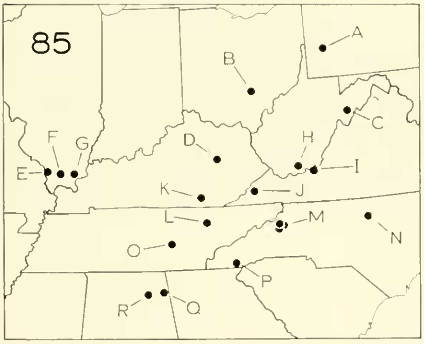

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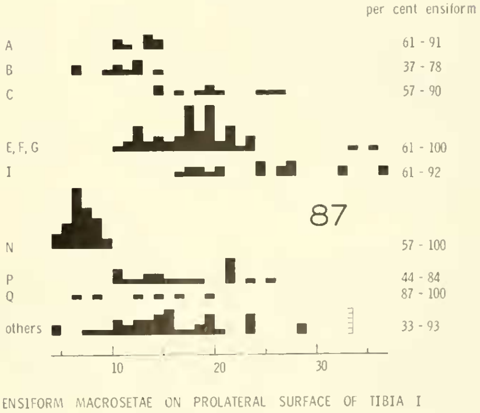

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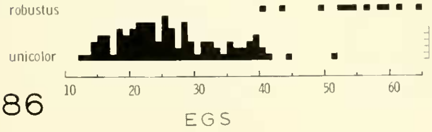

(In all subsequent population sample comparisons, dark individuals were excluded from sample *I* and light individuals from sample *K*.) Marked genetic heterogeneity within the light specimens is indicated by the divergence of sample *I*. This sample is clearly distinct from all other light samples in IVML/IML (Fig. 89), markedly different in a few other ratios (IVTL/CL, Fig. 93), and more similar in most characters to several of the dark samples. (Male sample *I*, which matches the light female *I* sample in color, is not divergent in any character studied.) Light samples *F*, *O*, *Q*, and *R* are quite similar to each other in almost all characters, and as a group differ most from the dark samples in ratios IFL/IVFL (Fig. 88) and IVML/IML (Fig. 89). However, at least one of these light samples exhibits considerable overlap with one or more dark sample in every character. Sample *O* is clearly the light sample most distinct from the dark samples. Sample *N*, which is intermediate in coloration (Fig. 92), more closely resembles dark samples in some characters and light samples in other characters and is not divergent in any character.

As with color, two setation characters revealed discontinuous intrapopulation variation. Three females from *K* differ distinctly from all other females in possessing extremely thick and short background setae on the posterior 1/3 of the abdomen. In addition, these three females have a distinctly lower IML/ItarL (Fig. 90), lower IVML/IVTarL, higher CMT/IVMT, longer thinner setae medially on the abdominal dorsum just behind the petiole, shorter denser abdominal background setae, and slightly more robust chelicerae than the other *K* females. Also the seminal receptacle stalk bases are not expanded (Fig. 277) as in the rest of sample *K* (Fig. 272). These three specimens even differ considerably from the rest of the species sample in IML/ITarL (Fig. 90), IVML/IVTarL, and the shape of the seminal receptacle stalks. The large variance of the whole of sample *K* in several characters (Figs. 88, 89) further illustrates its marked heterogeneity.

Females with very thick short setae on their sternum are found within several population samples (*M*, *P*, *L*, *D*) and as scattered individuals over a large part of the species' distribution range. Most other individuals possess only slender sternal setae; however, there are a few individuals intermediate in this character. Stout sternal setae are not found on light colored individuals. Comparisons of the stout sternal setae subsample to the slender setae subsample within each of samples *M* and *P*, and comparisons of the entirely stout setae sample *D* against each dark slender setae population sample were performed to discover if these sternal setae forms are distinct in other characters. Within each comparison at least a few ratios separated the two forms (Fig. 91), but few of these characters were common to all comparisons. Sample *D* is markedly divergent in several ratio characters from many other *A. unicolor* population samples (Figs. 88, 93). When all stout sternal setae individuals are compared to a large sample of dark colored slender sternal setae individuals, only IVFL/CL yields rather distinct separation (Fig. 91).

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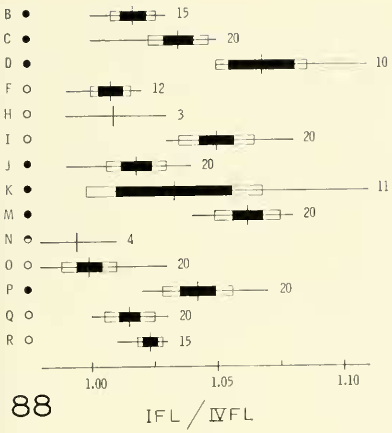
Figures 88–93. Geographic variation in *Antrodiaetus unicolor* females. (Dark colored samples identified by black dot, light samples by circle, and intermediate colored sample by half-blackened circle.) 88. Mod. Dice-Leraas diagram of IFL/IVFL variation. 89. Mod. Dice-Leraas diagram of IVML/IML variation. 90. Mod. Dice-Leraas diagram of IML/ITarL variation in sample with stout posterior abdominal background setae and samples with normal (slender) abdominal setae. 91. Mod. Dice-Leraas diagram of IVFL/CL variation in samples with stout sternal setae and samples with slender sternal setae. 92. Color variation. Frequency of pars cephalica color values given for each sample. (Key to color grid at lower right. Full explanation in Methods section.) 93. Mod. Dice-Leraas diagram of IVTL/CL variation.



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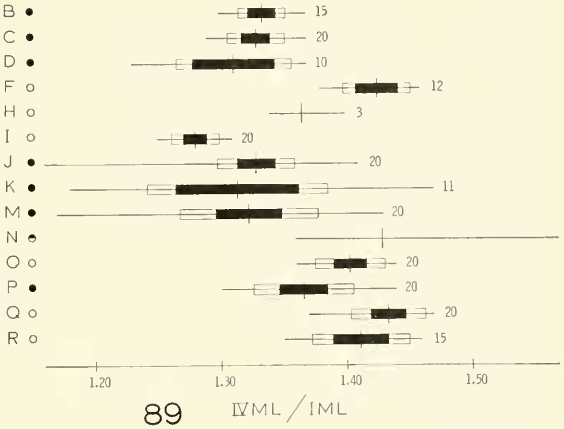

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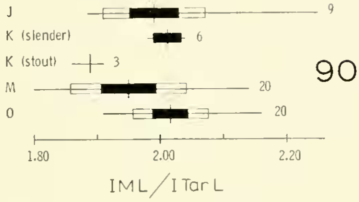

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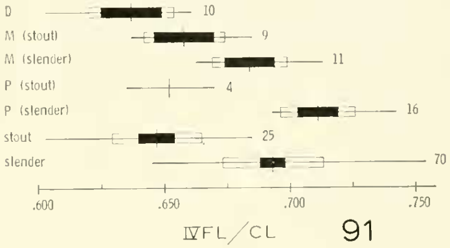

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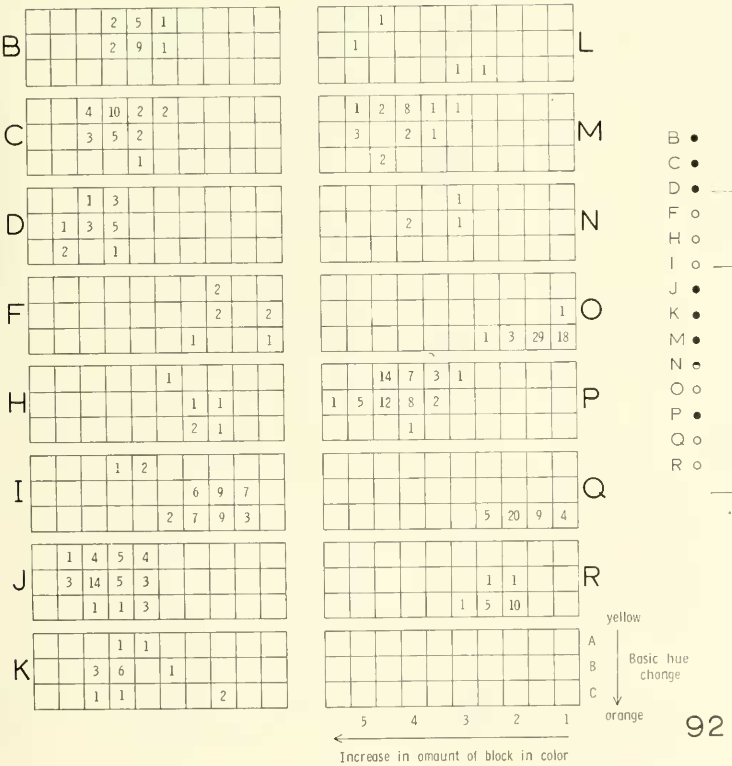


B				2	5	1				
				2	9	1				

C			4	10	2	2				
			3	5	2					
					1					

D			1	3						
		1	3	5						
		2		1						

F								2		
								2		2
							1			1

H						1				
							1	1		
							2	1		

I				1	2					
							6	9	7	
						2	7	9	3	

J		1	4	5	4					
		3	14	5	3					
			1	1	3					

K				1	1					
			3	6		1				
			1	1				2		

L			1							
		1								
						1	1			

M		1	2	8	1	1				
		3		2	1					
			2							

N						1				
				2		1				

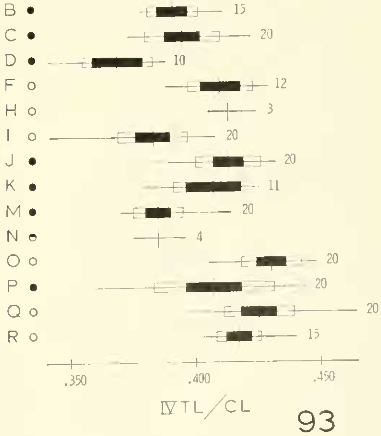
O										
										1
							1	3	29	18

P			14	7	3	1				
	1	5	12	8	2					
				1						

Q										
							5	20	9	4

R										
							1	1		
						1	5	10		

92



93

Noteworthy variation without a clear geographic pattern occurs in two other qualitative characters. While the great majority of females have short converging setae medially on the abdominal dorsum just behind the pedicel (Fig. 313), a few have here long slender setae (as in *A. robustus,* Fig. 314) or setae of intermediate length. Such aberrant individuals are scattered in several distantly separated dark population samples and are rare in light samples. No other characters vary concordantly with this one. Female genitalia are quite variable in this species, but the variation is continuous with a few exceptions. Figures 274 and 275 illustrate the wide variation apparently common even in a genetically relatively homogeneous population. Figures 270–279 illustrate much of the total variation found, and do not necessarily represent the modal structure for each population sample. Divergent seminal receptacle form was found only in the three *K* specimens with stout posterior abdominal background setae and in both dark specimens at *L*. In these, all seminal receptacles lacked expanded stalk bases (Fig. 277) and also resembled *A. robustus* receptacle form in some qualitative aspects.

Discussion. Variation in *A. unicolor* is somewhat complex and difficult to interpret. In addition to strong geographic variation patterns, there are also instances of different forms occurring sympatrically. It is conceivable that further studies may reveal convincing evidence that this series of populations consists of several reproductively isolated gene pools.

The two clearly divergent population samples (*A* and *N*) exposed in the analysis of variation of male characters are apparently genetically quite different from the other samples (and less different from each other) and each can be readily characterized by a combination of several characters. Both are clearly geographically peripheral populations presumably exchanging genes only at a relatively slow rate, with the sampled populations located in the region of greatest population density. A study of geographically intermediate populations is necessary to determine to approximately what degree (if any) gene exchange is occurring.

The possibility was examined that character divergence might be occurring between *A. unicolor* and *A. robustus* populations in the vicinity of *A* and that this might be partly responsible for the divergence of sample *A*. Sample *A* is markedly more different from the sympatric (Allegheny Co. and Westmoreland Co.) *A. robustus* males than are allopatric samples *B* and *C*—the pattern that could result from character divergence—in 10 ratios including PTT/PTL (Fig. 81), PFL/CL and OQW/CL. Several of the characters that best separate sample *A* from the other *A. unicolor* samples (IML/CL, ETL/CL [Fig. 84], IML/ITarL) either do not show this pattern or show the reverse pattern, and two other characters also show the reverse pattern. Thus, while some of sample *A's* uniqueness could be the result of character divergence, some cannot.

The significance of the color variation, discontinuous in the female samples, is difficult to determine. Considerable genetic heterogeneity exists within the total light sample and the entire dark sample. Upon removing the more divergent elements, the remaining light and dark samples are each still genetically rather heterogeneous and they differ, but are still not distinct in any character except color. It appears unlikely that the color forms are either geographic variants or ecophenotypes, since they are found together in the same general habitat in at least three localities. It is possible that these color forms are distinct species, but the absence of any other character which in many samples consistently matches the discontinuity in coloration argues against this. Perhaps the most feasible explanation is genetic polymorphism; if so, there would appear to be a surprisingly large number of populations in which fixation of one morph has occurred. Analysis of larger samples from localities where the forms are sympatric, close observation for microhabitat differences and local spatial separation of the forms, a study of color variation of adults reared from single broods, and a comparison of the physiological basis of coloration in the two forms are kinds of studies needed to solve this problem.

The specimens from *K* with stout posterior abdominal background setae are so distinct from the rest of the local sample that they may be reproductively isolated. The possibility of genetic polymorphism involving several characters or of ecological races cannot be ruled out presently. It is unlikely that age differences could produce discontinuity in so many characters in this sample and not in other samples. The divergence of sample *D* and the other specimens with very stout sternal setae from the rest of the dark specimens is assumed to represent simple intraspecific genetic variation because of the occurrence of a few intermediate individuals and because only one other character separates most of the individuals of these two forms. These divergent setation forms require further study along the lines suggested above. Particularly helpful would be collections of males from *K* and *D*.

Distribution. Centered in the central and southern Appalachian region of eastern United States with populations extending peripherally in all directions, as far west as the Ozark region and apparently south to near the Gulf Coast (Map 1).

Records. ALABAMA. *De Kalb Co.:* De Soto St. Pk. [*Q*], near Fort Payne, July–Aug. 1937, 2♂; Oct., ♂; Dec., ♂; 1800–1900 ft, 38♀. *Madison Co.:* Monte Sano St. Pk., Dec. 1940, ♂. *Marshall Co.:* Little Mtn. St. Pk. [*R*], 600–700 ft, 24♀. — 0.8 mi. N of Grant, ♀. ARKANSAS. *Stone Co.:* Blanchard Springs Rec. Area (USFS), 11 Sept. 1966, ♂, 2♀. GEORGIA. *Fulton Co.:* Atlanta, 14 Nov. 1945, ♂. *Murray Co.:* Fort Mtn. St. Pk., approx. 2400 ft, ♀. *Rabun Co.:* Rabun Bald, 15♀. *Towns Co.:* Brasstown Bald Mtn., 4700 ft, ♀. ILLINOIS. *Jackson Co.:* Little Grand Canyon, ♀. *Johnson Co.:* Ferne Clyffe St. Pk. [*F*], approx. 800 ft, 13–14 Sept. 1966 (♂), ♀; 1 Oct. 1967, 2♂; 12♀. *Pope Co.:* Lusk Creek [*G*], 28 Sept.–5 Oct., ♂; 5–12 Oct., 7♂; 12–19 Oct., ♂; 26 Oct.–2 Nov., ♂ (all in 1968). *Union Co.:* Pine Hills [*E*], 7–14 Oct., 11♂; 14–20 Oct., 2♂; 20–27 Oct., ♂; 27–30 Nov., ♂ (all in 1967). INDIANA. *Jefferson Co.:* Clifty Falls St. Pk., 2♀. KENTUCKY. *Edmonson Co.*: Mammoth Cave Natl. Pk., 600 ft, 2♀. *McCreary Co.:* Cumberland Falls St. Pk. [*K*], 5♀. *Powell Co.:* Natural Bridge St. Pk. [*D*], 12♀. *Whitley Co.:* Cumberland Falls St. Pk. [*K*], 7♀. MARYLAND. *Montgomery Co.:* Plummers Island, 24 Oct. 1909, ♂. NEW JERSEY. *Bergen Co.:* Closter, ♀. NEW YORK. *Bronx:* Bronx Park, 21 Oct. 1954, ♂. NORTH CAROLINA. *Avery Co.:* between Edgemont and Linville along Gragg Prong Cr. [*M*], 2300 ft, 5♀. *Burke Co.:* Linville Falls [*M*], 3100 ft. 15♀. *Caldwell Co.:* 5 mi. E of Mortimer [*M*], 1500 ft, 4♀. *Durham Co.:* Duke Forest [*N*], approx. 500 ft, 1 Oct., ♂; 22 Oct., ♂; 23 Oct., 2♂; 24 Oct., 11♂; 7 Nov., 2♂; 3 Jan., ♂ (all in 1963–64); 4♀. *Haywood Co.:* Mt. Pisgah, Frying Pan Gap, 13 Oct. 1926, ♂. *Jackson Co.:* 5 mi. E of Bryson City, 2 Oct. 1960, ♂. *Macon Co.:* Highlands [*P*], 1–3 Aug. 1966, 4300 ft, 8♂, 53♀; 24 July 1962, ♂. — Whitesides, Cove Church [*P*], 22 Aug. 1962, ♂. *Transylvania Co.:* Bear Wallow. 2♀. OHIO. *Adams Co.:* Long Lick Hollow, 2♀. *Hocking Co.:* Ash Cave St. Pk. [*B*], approx. 800 ft, 30 Sept. 1962, ♂; 22 Sept. 1966 (♂); 6 July 1966 (♂); 18♀. — Cantwell Cliffs St. Pk. [*B*], 6 July 1966 (♂), 6♀; ♂. PENNSYLVANIA. *Allegheny Co.:* Penn Hills [*A*], 12–13 Sept. 1963, 2♂; 26 Sept. 1963, ♂; 2♀. — Pittsburgh [*A*], Oct. 1960, ♂. SOUTH CAROLINA. *Oconee Co.:* Five Point Cave, 4 mi. N of Westminster, ♀. TENNESSEE. *Anderson Co.:* on rt. 116, 12–24 mi. W of Lake City [*L*], 30–31 Aug.

1966, ♂, 4♀. *Chester Co.:* Chickasaw St. Pk., 600–700 ft, ♀. *Cocke Co.:* Great Smoky Mtn. Natl. Pk., near Cosby Camp, 2200 ft, 5–14 Aug. 1966, 2♂. *Hamilton Co.:* Signal Mtn., ♀. *Lawrence Co.:* David Crockett St. Pk., 700–900 ft, 2♀. *Sevier Co.:* Great Smoky Mtn. Natl. Pk., Laural Creek, ♀. — Elkmont, ♀. — Clingmans Dome, 6000–6600 ft, 10–14 Aug. 1966, 2♂. — Greenbrier Cove, 7–8 mi. NE of Gatlinburg, 2 Oct. 1960, 2♂. *Sullivan Co.:* Bristol, 5 Oct. 1926, ♂. *Van Buren Co.:* Fall Creek Falls St. Pk. [*O*], 1500–1600 ft, 1 Sept. 1966, ♂, 48♀. VIRGINIA. *Dickenson Co.:* Breaks Interstate Pk., ♀. *Fairfax Co.:* on bank of Potomac R. opposite Plummers Island, Sept. 1918, ♂. *Giles Co.:* Mountain Lake [*I*], 3900 ft, 21 Aug. 1966, 9♂; 14 Aug. 1948, ♂; 45♀. *Montgomery Co.*: Radford, Oct. 1967, ♂. — Blacksburg, 23 Oct. 1961, ♂; 28 Oct. 1956, ♂. *Wise Co.:* few mi. S of Tacoma [*J*], approx. 2400 ft, 28♀. — Several mi. S of Tacoma, Osborne Rock [*J*], approx. 3600 ft, 20♀. WEST VIRGINIA. *Mercer Co.:* Brush Creek Falls, 3 Oct. 1966, ♂. — Athens [*H*], 2400 ft, 3♀. *Pendleton Co.:* Briggs Run near Smoke Hole [*C*], 1500 ft, 14–16 Aug. 1966, 5♂, 24♀. *Pocahontas Co.:* Cranberry Glades Nat. Area (USFS), ♀. *Raleigh Co.:* Grandview St. Pk., 23 Sept. 1967, ♂; 3♀. *Webster Co.:* 1 mi. S of Cleveland, ♀. *Wyoming Co.:* Mullins, ♂.

The following geographically important records of immature specimens, probably *A. unicolor*, are indicated on Map 1 with circles. ALABAMA. *Clark Co.:* 2 mi. N of Jackson. *Conecuh Co.:* W Fort Sapulga R. *Coosa Co.:* Hatchet Creek. LOUISIANA. *E. Feliciana Parish.* NORTH CAROLINA. *Yancey Co.*: Mt. Mitchell, 6600 ft. SOUTH CAROLINA. *Greenville Co.:* Paris Mtn. St. Pk. TENNESSEE. *Bedford Co.:* outside Reese Cave. *Madison Co.:* Bonwood. VIRGINIA. *Grayson Co.:* Mt. Rogers, 5000–5600 ft. *Page Co.:* Stony Man Mtn. *Pittsylvania Co.:* Smith Mtn. Gorge, N of Sandy Level.

Antrodiaetus robustus (Simon)

Figures 139, 159, 195–196, 241–243, 280–283, 314, 316–317. Map 1.

Brachybothrium robustum Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 311. Male and female syntypes (one each). The female specimen, which I have examined, is here designated and labeled the lectotype and is in the U. S. National Museum. The male paralectotype may be in the U. S. National Museum or may be lost. (See comments below on the designated type localities.) –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet (in part), 1955, Bibliographia Araneorum, 2: 907.

Brachybothrium shoemakeri Petrunkevitch, 1925, Ann. Ent. Soc. America, 18: 318, pl. 20, figs. 3, 5, 6, 11. Five male syntypes and an immature female syntype from "different localities near Washington, D. C., on the Virginia bank of the Potomac River"; 2 males examined. The male collected on the Virginia bank of the Potomac River a short distance above Georgetown (Washington, D. C.), 27 Sept. 1911, by C. R. Shoemaker, is here designated and labeled the lectotype and is in the Yale Peabody Museum. The one examined paralectotype male is in the American Museum of Natural History. (See comments below on these specimens.) NEW SYNONYMY. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 907.

Antrodiaetus robustus: Gertsch and Mulaik, 1940, Bull. American Mus. Nat. Hist., 77: 311.

Antrodiaetus shoemakeri: Muma, 1944, American Mus. Novitates, (1257): 1; examined.

Antrodiaetus unicolor: Vogel, 1966, Jour. New York Ent. Soc., 74(1): 56; examined. –Vogel, 1968, Jour. New York Ent. Soc., 76(2): 101; examined.

Antrodiaetus accentuatum: Snetsinger and Whitmyre (in part), 1967, Science for the Farmer, 14(4): 5, 2 photos; examined. –Whitmyre and Snetsinger (in part), 1967, Melsheimer Ent. Series, No. 1, p. 1, figs. 1–7; examined.

Comments on the descriptions. The male paralectotype of *B. robustum* is not in the Muséum National d'Histoire Naturelle in Paris where all types of the other *Antrodiaetus* species described by Simon are deposited. Simon's (1890) description does not help to identify the male. The designated type locality for the female is almost certainly wrong. Simon listed together two localities, "Virginia, Occoquan Falls (G. Marx); Texas: Rio-Grande (G. Marx)," after the type descriptions and failed to indicate which specimen came from which locality. Since the locality on the label with the female is "Columbus, Texas," the male is presumably from the Virginia locality. Why Simon designated Rio Grande rather than Columbus is unclear. Gertsch and Mulaik (1940), who cited this record, assumed that Simon meant the town of Rio Grande City in Starr County, Texas, about 270 miles southwest of Columbus. Since these Texas localities are at least 1100 air miles southwest of the nearest known population of this species, since the habitats in this area are extremely different from the known northern habitat, and since George Marx (who accumulated and sent the specimens to Simon) often gave specimens wrong locality labels (H. Levi, personal communication), I shall assume that both the label with the female lectotype and the type locality designated by Simon are wrong. The real locality is most likely near Washington, D. C., which is in the known species range, is near the designated locality for the male specimen, and is near Marx's home.

Since Petrunkevitch (1925) did not designate a holotype for *B. shoemakeri*, I have designated as lectotype the specimen on whose label he wrote "Type." The only other paralectotype known to me is accompanied by a label with the word "cotype" in Petrunkevitch's handwriting. This paralectotype male is a misidentified *A. unicolor.*

Figures 1, 2, and 3 in Whitmyre and Snetsinger (1967) are definitely of *A. robustus.* The sternal sigilla, described and figured as being "lighter colored areas," are normally slightly darker than the surrounding cuticle as in all other antrodiaetids. The i.c.s. tip in Figures 6 and 7 is apparently broken off.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the lectotype.

Male. Carapace: Very few setae on pars thoracica except along lateral border. *Chelicerae:* Rather large setaless area on upper ectal surface. *Pedipalps:* Figures 195, 196. Tibia moderately swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus pointed; closely appressed to i.c.s. Tip of i.c.s. relatively wide; well sclerotized except for translucent area on side against o.c.s. *Leg I:* Figures 241–243. Group of attenuate (occasionally 1 is ensiform) macrosetae centered at 1/2 to 2/3 of distance from proximal to distal end of tibia on prolateral surface. Fewer, more scattered, attenuate (occasionally 1 is ensiform), frequently larger macrosetae along retrolateral aspect of ventral surface; distalmost macroseta of this group positioned at 3/4 or more of distance from proximal to distal end of tibia. One to 8 attenuate macrosetae scattered on ventral surface between these two groups. Tibia nearly cylindrical. One to 3 macrosetae (usually 2) ventrally at distal end of metatarsus. Metatarsus slightly sinuous in ventral view. *Abdomen:* 3 dorsal heavily sclerotized patches. First and second large and usually continuous; posterior patch smallest and usually reduced to transverse row of 2 or 4 small patches. Minute sclerotized scar or bump usually located anterior and ectal of each PM spinneret. *Coloration:* Carapace gray-yellow to brown; pars cephalica usually darker than pars thoracica. Sternum and pedipalpal coxae pale gray-yellow to pale gray-orange; labium darker gray-yellow to brown. Chelicerae similar to or slightly darker than pars cephalica. Patella, tibia, and metatarsus of leg I gray-orange to dark red-brown; femur slightly lighter dorsally and much lighter ventrally. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen yellow-gray to medium gray-brown; dorsal sclerotized patches darker except sclerite of second patch often similar to pars thoracica.

Female. Carapace: Setae sparse on pars thoracica, denser along lateral border. All pars thoracica setae very slender. *Sternum:* Figure 139. Relatively broad. *Chelicerae:* Figure 159. Microteeth positioned beside last 6 to last 4 macroteeth; usually extend beyond last macrotooth. Microteeth proportionately large. Large setaless area on upper ectal surface. *Abdomen:* Figures 314, 316, 317. Dorsal background setae densely distributed; moderately short and basally somewhat thickened. Convergent median dorsal setae just posterior to pedicel long and slender. Minute sclerotized scar or bump (probably a vestige of AL spinnerets) located anterior and ectal of each PM spinneret; usually a setaless area posterior of bump. *Genitalia:* Figures 280–283. Seminal receptacles with well-sclerotized stalk and bowl; vary from moderately long and moderately thick to quite stout. Stalk not expanded at base. Bowl well developed; its border with bulb sharply defined. Floor of bursa copulatrix moderately well sclerotized. *Coloration:* Carapace gray-orange to chestnut brown; pars cephalica usually darker than pars thoracica. Sternum similar to pars thoracica; labium and pedipalpal coxae slightly darker than pars cephalica. Chelicerae medium brown to dark red-brown; darker than pars cephalica. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen light brown to medium brown; tergite similar to pars thoracica.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 241–243; Table 12) are distinctive for this species. The three important differences in these characters from the similar sympatric species *A. unicolor* are: 1) 8 per cent or fewer of the prolateral tibial macrosetae are ensiform. 2) The distalmost macroseta on the retrolateral aspect of the ventral surface of the tibia is 3/4 or more of the distance from the proximal to distal end (only rarely this near the distal end in *A. unicolor*). 3) Metatarsus I macroseta B is almost always present. The partly translucent i.c.s. tip (Fig. 195) helps identify *A. robustus.* Also the i.c.s. tip is usually wider and usually extends proportionately less beyond the o.c.s. tip (Fig. 195) than in *A. unicolor,* but *A. robustus* cannot be separated from the sympatric Pittsburgh, Pennsylvania, area *A. unicolor* population with these two characters (Fig. 84). High EGS number is also an aid in identifying *A. robustus* (Fig. 86). No other quantitative characters studied help separate these two species. The same measurements and ratios useful in separating *A. unicolor* from the other *unicolor* group species are likewise useful in distinguishing *A. robustus* from these species. The presence of vestiges of AL spinnerets may be diagnostically useful, but a few *A. robustus* males appear to lack these and occasionally *A. unicolor* males have these vestiges.

Females. The combined presence of AL spinneret vestiges (Fig. 317), rather short densely distributed dorsal abdominal background setae (Fig. 316), and thin elongate setae medially and dorsally just posterior of the pedicel (Fig. 314), distinguish this species from other *unicolor* group species. The seminal receptacle stalks are not expanded basally (Figs. 280–283) as is common in *A. unicolor* and some other species. The sternum is proportionately wide, so that SL/SW (Fig. 139; Table 14) helps separate this species from *A. unicolor* and several others. Also metatarsi I and IV and tibia I are proportionately shorter than in *A. unicolor* and some other *unicolor* group species. Therefore IFL/IML, IML/CL, and IVML/CL are diagnostically useful (Table 14). *A. robustus* females usually have larger cheliceral microteeth than do *A. unicolor* females (Fig. 159).

Variation. Only moderate variation occurs in most characters studied for both sexes of *A. robustus. Males.* All specimens have an ETL/CL of .023 or less except one male (from Whitehall, Pennsylvania), which has an ETL/CL of .027 (Fig. 84). There is wide variation in the total number of macrosetae on the prolateral surface of tibia I, but the proportion of these which are ensiform varies only slightly (Table 12). *Females.* Relatively wide but continuous variation occurs in the thickness of the seminal receptacle stalk relative to bowl diameter (Figs. 280–283). The shape of the bursa copulatrix floor also varies considerably.

Discussion. A. robustus is extremely similar to *A. unicolor* in nearly all characters studied; these constitute the most morphologically similar pair of *Antrodiaetus* species and perhaps deserve to be called sibling species. Were these two populations allopatric, I probably would conclude that they are conspecific. That they are sympatric (intimately so in at least the Pittsburgh, Pennsylvania, and Washington, D. C., areas) and appear to remain distinct in the several diagnostic characters is strong evidence that they are reproductively isolated populations. However, the possibility that *A. robustus* is a northern genetic variant form of *A. unicolor* cannot be confidently ruled out without more data, chiefly from studies of variation on larger samples of both species from additional localities in the area of sympatry.

In this context, the following instance of variation within an otherwise homogeneous population sample of *A. unicolor* is noteworthy. One aberrant male in a Lusk Creek (Pope Co.), Illinois, sample with nine other *A. unicolor* males has an i.c.s. tip width, an ETL/CL value, a distalmost ventral-retrolateral tibia I macroseta position, A and B metatarsal macrosetae, and a pointed o.c.s. tip all as in *A. robustus.* The part of the i.c.s. tip against the o.c.s is very slightly translucent and therefore intermediate. However, over 50 per cent of its prolateral tibia I macrosetae are ensiform, and 50 per cent of its ventral-retrolateral tibia I macrosetae are ensiform, both diagnostic *A. unicolor* character states.

Distribution. Pennsylvania, Maryland, northern Virginias, and eastern Ohio (Map 1).

Records. MARYLAND. *Allegheny Co.:* Hagerstown, ♀. *Montgomery Co.:* Chevy Chase, ♀. *Prince Georges Co.:* College Park, 15 Oct. 1942, ♂. OHIO. *Stark Co.:* Canton, 28 Sept. 1941, ♂, ♀. PENNSYLVANIA. *Adams Co.:* Caledonia St. Pk., 5♀. *Allegheny Co.:* Whitehall, Sept. 1966, ♂. — Penn Hills, 3♀. — Baldwin, ♀. — Verona, ♀. — Mt. Troy, ♀. *Westmoreland Co.*: Powdermill Nature Reserve, 3 mi. S of Rector, 6 Sept. 1962, ♂; 11 Oct. 1962, ♂; 19 Oct. 1966, 4♂; 19 Oct.–13 Nov. 1966, ♂. — 2 mi. NE of Ligonier, 12 Sept. 1963, ♂. VIRGINIA. *Fairfax Co.:* on bank of Potomac R. a short distance above Georgetown (Washington, D. C.), 27 Sept. 1911, ♂. *St. Marys Co.:* Tall Timbers, 24 Oct. 1927, ♂. WEST VIRGINIA. *Ohio Co.:* Wheeling, Oct. 1947, ♂.

Antrodiaetus pacificus (Simon)

Figures 121–122, 131, 147–149, 160, 170, 175–177, 197–203, 244–247, 284–291. Map 2.

Brachybothrium pacificum Simon, 1884, Bull. Soc. Zool. France, 9: 314. Syntypes (1 male and 1 possibly immature female) from Washington Territory in the Pacific Northwest; in the Muséum National d'Histoire Naturelle in Paris; examined. The male specimen is here designated the lectotype and the female the paralectotype, and they are so labeled. –Worley, 1928, Ann. Ent. Soc. America, 21(4): 619, fig. 2. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet (in part), 1955, Bibliographia Araneorum, 2: 335.

Antrodiaetus hageni: Gertsch and Jellison (not Chamberlin, 1917), 1939, American Mus. Novitates, (1032): 1.

Antrodiaetus pacificus: Chamberlin and Ivie, 1941, Bull. Univ. Utah, 31(8): 3. –Thorn, 1967, British Columbia Prov. Mus. Annual Report, p. 1. (*Antrodiaetes*).

Comment on lectotype. The lectotype male clearly matches in all characters the males in the western (coastal) populations of *A. pacificus.* It was therefore probably collected in western Washington as Simon (1884) apparently meant to indicate by adding "(Pacifique)" to his type locality designation.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the lectotype. In order to avoid contamination of the female *A. pacificus* species sample by *A. occultus* females (which probably are very similar to *A. pacificus*), no females from the area of sympatry of these two species are included in the *A. pacificus* sample studied (except for females from two burrow aggregations containing only *A. pacificus* males).

Male. Carapace: Figures 121, 122. Setae sparse on pars thoracica except usually moderately dense along lateral border. *Chelicerae:* Figures 147–149. Usually a large setaless area on upper ectal surface; occasionally this area small. *Pedipalps:* Figures 175–177, 197–203. Tibia moderately swollen in lateral view; greatest diameter in lateral view at between 1/3 to 1/2 of distance from proximal to distal end. Tip of o.c.s. of palpus rounded (blunt) and closely appressed to i.c.s. I.c.s. tip well sclerotized; usually weakly to moderately curved. *Leg I:* Figures 244–247. Dense, often large group of macrosetae (usually none, rarely a few, ensiform) on prolateral surface of tibia, centered at between 1/2 to 2/3 of distance from proximal to distal end. Other macrosetae (usually none or 1, rarely most, ensiform) scattered along retrolateral aspect of ventral surface of tibia with distalmost macroseta positioned at 3/4 or more (usually more) of distance from proximal to distal end. Often 1 to a few macrosetae scattered ventrally between these two groups. Tibia usually slightly swollen at prolateral macrosetae group. No macrosetae on metatarsus (very rare exceptions). Metatarsus elongate; usually weakly sinuous in ventral view. *Abdomen:* Usually 3 noncontinuous dorsal heavily sclerotized patches; posterior usually smallest and varies greatly in size. *Coloration:* Carapace gray-yellow to medium red-brown; pars cephalica often slightly darker than pars thoracica. Sternum pale gray-yellow; pedipalpal coxae slightly darker; labium darker yellow-gray to brown. Chelicerae similar to or slightly lighter than carapace. Patella, tibia and metatarsus of leg I medium to very dark red-brown, much darker than carapace; femur dorsally almost as dark as these segments, ventrally much lighter. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale gray-yellow to dark purple-gray; often darkest dorsally posterior of sclerotized patches. Occasionally this dark area chevron patterned. Sclerotized patches often similar to, sometimes darker than, carapace.

Female. Carapace: Figure 131. Setae sparse to moderately dense over most of pars thoracica; moderately dense to dense along lateral border. *Chelicerae:* Figures 160, 170. Microteeth positioned beside last 8 to last 3 macroteeth; often extend beyond last macrotooth. Microteeth proportionately small to medium size. Large to medium size setaless area on upper ectal surface. *Abdomen*: Background setae on dorsum distributed sparsely to moderately densely. *Genitalia:* Figures 284–291. Seminal receptacles evenly spaced or paired; with well-sclerotized stalk and bowl; stout to slender (much variation). Stalk base sometimes expanded. Bowl usually well developed; its border with bulb sharply defined. Floor of bursa copulatrix moderately to very weakly sclerotized; sometimes constricted medially. *Coloration:* Carapace pale gray-yellow to chestnut brown; pars cephalica usually slightly darker than pars thoracia. Sternum similar to pars thoracica; pedipalpal coxae similar to pars cephalica or darker; labium dark gray-orange to dark brown. Chelicerae gray-orange to dark red-brown; darker than pars cephalica. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen light yellow-gray to dark purple-gray; sometimes much darker dorsally than elsewhere; occasionally this dark area chevron patterned. Tergite similar to pars thoracica.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 244–247; Table 12) are distinctive for this species and include some of the best characters for identification. *A. pacificus* (especially the western populations) has a proportionately long metatarsus I and short tibia I, so that ITL/IML (and often IFL/IML, ITL/ITarL, and IML/ITarL) provides clear separation from several other *unicolor* group species (Figs. 94, 244; Table 13). Because of a proportionately long pedipalpal femur, *A. pacificus* can be separated from some species by the ratio PFL/CL (Table 13). The o.c.s. tip of the palpus is much more rounded than that of *A. pugnax* or *A. hageni,* and much more closely appressed to the i.c.s. than that of *A. occultus* (Figs. 197–203).

Females. As described in the *A. hageni* and *A. montanus* diagnoses, cheliceral and carapace setation, cheliceral microteeth size, and coloration are usually helpful in separating *A. pacificus* females from these two species (Figs. 160, 170). IVML/IML (Table 14) helps distinguish *A. pacificus* from *A. pugnax* and *A. cerberus;* metatarsus I is relatively longer and metatarsus IV relatively shorter in *A. pacificus.* Because IFL is proportionately long and IVFL relatively short in *A. pacificus,* IFL/IVFL and occasionally related ratios (Table 14) are diagnostically helpful. *A. pacificus* has a significantly lower IVTL/CL value (Table 14) than *A. hageni* or *A. montanus.* The paired nature (Figs. 288–291) of the seminal receptacles in eastern *A. pacificus* specimens is not found in any other *unicolor* group species.

Variation. Numerous characters exhibit marked geographic variation, and in nearly every case the general pattern is the same —the population samples (*R–W*) from the Blue Mountains of northeastern Oregon and adjacent Washington are similar to one another and divergent from the western (*A–M*) samples, while the Idaho samples (*X–Z*) are either intermediate or similar to one of these two groups of samples (Fig. 98).

Males. Much of the strongest and most nearly discontinuous geographic variation is found in the ratio characters ITL/IML (Fig. 94), IFL/ITL (Fig. 95), ALD/CL, AMS/CL, ALD/ALS, ITL/CL, AMD/AMS, and AMD/CL (listed in order of degree of discontinuity). Sample *W* and usually also samples *R–V* and *X* are clearly divergent from the other samples, particularly in the first six of these ratios. Individuals in these samples usually have a proportionately longer ITL (Figs. 244, 247) and proportionately smaller and more widely separated ALE and AME (Figs. 121, 122) than males of other samples. In a few of these ratio characters, samples *R–V*, Z, and *M* are intermediate between sample W and the western samples, but in most characters samples Z and *M* are similar to the western samples. Several measurements, particularly ITL (Fig. 94) and CL (Fig. 97), exhibit rather strong but continuous geographic variation; most exhibit similar geographic patterns presumably because of strong correlation with body size. Several characters—PTT/PTL (Fig. 96), ALD/ALS, and ALD/CL—exhibit the variation pattern that could result from character divergence between *A. pacificus* and *A. occultus.*

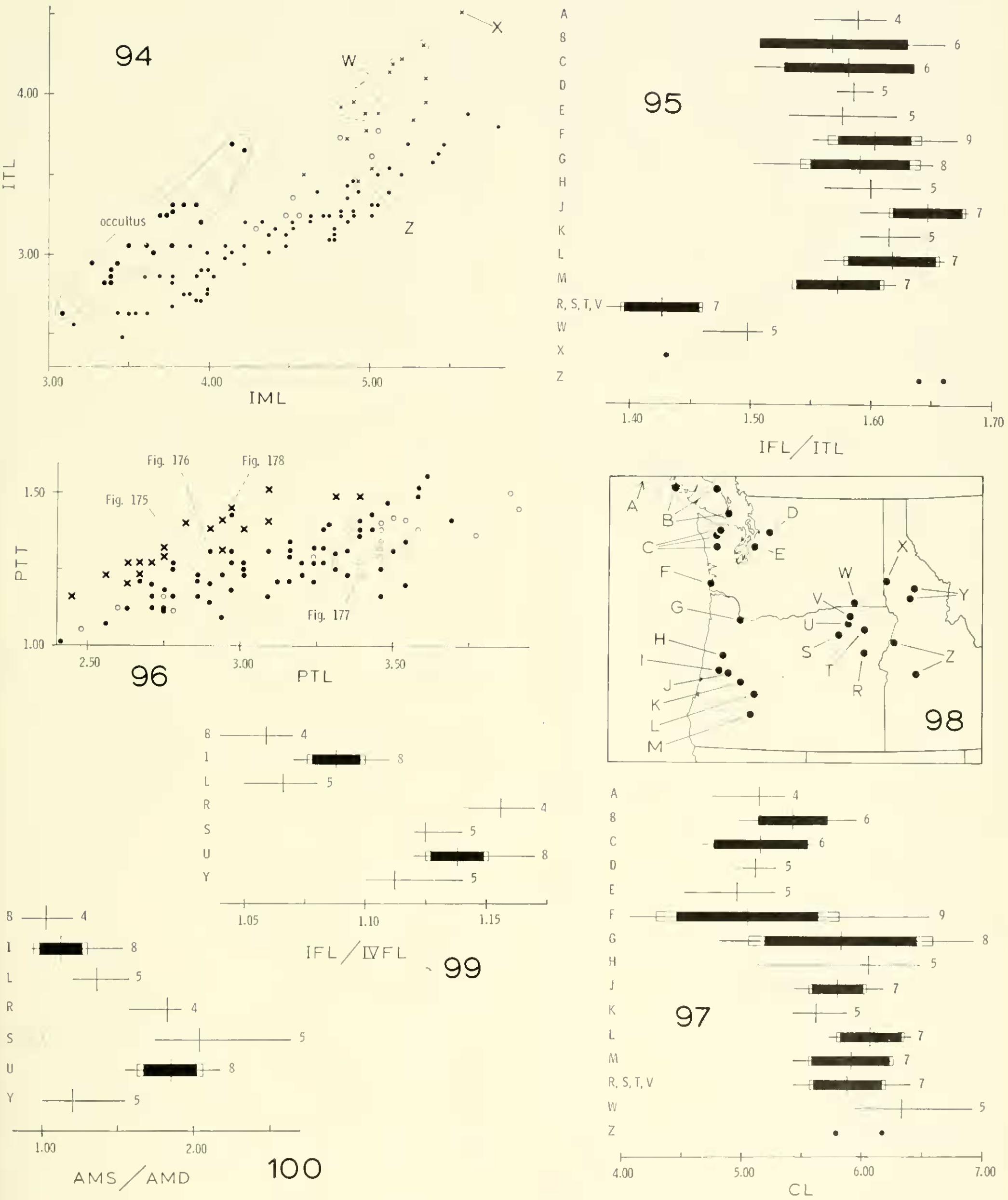
Individuals of samples *R–X* usually have a greater percentage of ensiform macrosetae in both the prolateral (0–27% ensiform vs. 0–3%) and ventral-retrolateral (8–100% ensiform vs. 0–33%) tibia I macrosetae groups than do individuals of all other samples (Figs. 244, 247). The tibia I prolateral macrosetae group is positioned slightly more proximally in samples *R–X* than in all other specimens (Figs. 244, 247). Individuals from *R–W* lack macrosetae on the ventral surface of tibia I between the two macrosetae groups, whereas specimens from *X* and *Z* and the majority of the rest of the samples have scattered small macrosetae in this position (Figs. 244, 247). The only three *A. pacificus* specimens with metatarsal macrosetae (Fig. 246) are from samples *T* and *X*. The i.c.s. tip of the palpus is usually more curved and more slender, the o.c.s. always wider, and the sperm reservoir often narrower in samples *R–W* than in the western samples (Figs. 201–203). The two Z males match the western males in palpus structure, whereas the *X* male is clearly intermediate in these characters. Specimens from *R–W* have smaller setaless areas on the upper ectal cheliceral surface than do all other individuals.

Females. The ratios IFL/IVFL (Fig. 99), AMD/CL, ALS/AMS, and AMS/AMD (Fig. 100) exhibit strong, nearly discontinuous geographic variation with samples *R, S,* and *U* differing considerably from the western samples (*B, I,* and *L*) and with sample *Y* either intermediate or similar to the western samples. Femur I is longer relative to femur IV length and the AME's are proportionately smaller and more widely separated in the Blue Mountain area samples (*R, S,* and *U*) than in the others. A few nonratio quantitative characters, particularly AMD, IVMT, and ITarL, also exhibit rather marked geographic variation, usually of a pattern similar to that of the above ratio characters.

There is remarkably strong variation in female genitalia morphology; much of it is geographic, with the Idaho and eastern Oregon females differing from the western specimens in the following ways (Figs. 288–291): 1) Seminal receptacles usually more or less distinctly paired with the ducts of the two inner receptacles not joining versus seminal receptacles not paired and ducts of inner receptacles usually joining. 2) Outer receptacles usually smaller than inner receptacles versus outer and inner receptacles same size or almost so. 3) Seminal receptacles usually more slender with proportionately longer stalk versus seminal receptacles stout with relatively short stalk. 4) Bursa copulatrix usually bilobed anteriorly versus not bilobed. However, there is much variation within sample S (Figs. 288–290), including two (Fig. 288) individuals with intermediate, nearly western-type genitalia. The females from eastern Oregon have markedly smaller setaless areas on the upper ectal surface of the chelicerae than do those of both the western and Idaho samples, which are similar in this character.

This analysis of variation strongly suggests that the Blue Mountains population (represented by samples *R–W*) and the western population of *A. pacificus* are genetically quite different; there is apparently little gene exchange between these two major populations. Also, records indicate that these populations are geographically isolated. It is doubtful that connecting populations could now exist in the dry, unfavorable region to the south, west, and directly north of the Blue Mountains population. If the Idaho populations were unknown, there would be little hesitancy in describing the Blue Mountains population as a distinct species, cognate with *A. pacificus.* However, the intermediate and frequently near-western phenotype of the Idaho samples is evidence that the Idaho populations are (or, until recent times have been) exchanging genes with both the Blue Mountain population and the western populations. If the eastern and western populations are presently connected, it is probable that the connecting populations will be found in a northern arc in the mountains of northern Idaho and along the British Columbia-Washington border where the habitat appears favorable for *A. pacificus* and where there has been very little searching for *Antrodiaetus.* Clearly these populations are worthy of further study.

Noteworthy, largely nongeographic variation occurs in several characters. The form of the male anterior-dorsal cheliceral protuberance is highly variable. Nearly the entire species variation range occurs within several single population samples.



Figures 94–100. Geographic variation in *Antrodiaetus pacificus*. (All measurements in mm.) 94–97. Males. 94. Scatter diagram of ITL and IML. (X's represent samples *R–Z*, circles sample *M*, small black dots rest of samples, and large black dots *Antrodiaetus occultus* males.) 95. Mod. Dice-Leraas diagram of IFL/ITL variation. 96. Scatter diagram of PTT and PTL. (Circles represent *A. pacificus* males sympatric with *A. occultus*, black dots rest of *A. pacificus* males, and x's *A. occultus* males.) 97. Mod. Dice-Leraas diagram of CL variation. 98. Map of population sample localities. 99–100. Females. 99. Mod. Dice-Leraas diagram of IFL/IVFL variation. 100. Mod. Dice-Leraas diagram of AMS/AMD variation.

Figure 147 illustrates a prominent protuberance (one which might function like the apparently homologous cheliceral apophysis of *Atypoides*), Figure 148 illustrates a modal *A. pacificus* cheliceral protuberance, and Figure 149 represents the low end of the range of variation in this character. Figures 96 and 175–177 illustrate the continuous variation in the shape of the pedipalpal tibia. Usually there are three noncontinuous sclerotized patches on the male abdominal dorsum, with the posterior patch smallest but varying greatly in size. Occasionally this third patch is reduced to a bilateral pair of sclerotized spots; on rare occasions it is absent. Occasionally in the western samples and usually in the Blue Mountains samples the three sclerotized patches are continuous.

Distribution. The Pacific coast of North America from San Francisco Bay north to southern Alaska, with outlying, perhaps isolated, populations in the montane areas of western Idaho, northern Oregon, and adjacent Washington (Map 2). Noteworthy locality records (not shown on Map 2) of immatures that are almost certainly *A. pacificus* are: Marin and Sonoma Counties, California, and Terrace, British Columbia (near the southern tip of Alaska).

Records. ALASKA. Ketchikan [*A*], 18–28 July 1951, ♂; 23 Aug. 1952, ♂; 27 July 1951, ♂; summer 1937, ♂. BRITISH COLUMBIA. *Vancouver Island* [*B*]: Victoria, 17 Aug. 1966, ♂; 30 July 1967, ♂; 3 Sept. 1966, ♂; 27 Oct. 1934, ♂; 18 Nov. 1928, ♂; 2♀. — Sidney, 10 Sept. 1967, ♂. — Esquimalt, 30 Aug. 1947, ♂. — Tofino, 7–15 Aug. 1953, ♂; 22 June–12 July 1950, ♂; 2♀. — Wellington, 15–31 Aug. 1951, 5 Oct. 1949, 15 Aug. 1949, 3♂; 2♀. — Nanaimo, 13 Sept. 1935, ♂. — French Creek, 6 Sept. 1949, ♂. — Caledonia, Kyuquot Sound, ♀. — Kyuquot, ♂; 29 July 1931 (♂); 17 Aug. 1958, ♂, ♀; 31 Sept., ♂. — Kyuquot, Weave's Island, 2♀. — Kyuquot, Spring Island, ♀. *Queen Charlotte Islands:* Frederick Island, 2♀. — Yalcoun River, 11 Aug. 1961, ♂. CALIFORNIA. *Humboldt Co.:* Miranda, 3 June 1936, ♂, ♀. *Mendocino Co.:* Piercy, ♀. — Russian Gulch St. Pk. near Mendocino, 2♀. *Trinity Co.:* Carrville, July 1934, ♂. IDAHO. *Adams Co.:* Bear [Z], ♂. *Boise Co.:* Lost Lake [Z], 27 July 1939, ♂. *Clearwater Co.:* Pierce [Y], 3♀. *Idaho Co.:* Kamiah [Y], 2000 ft, 2♀. *Latah Co.:* Moscow Mtns. near Moscow [X], June 1936, ♂. OREGON. *Baker Co.:* Marble Creek Picnic Area (USFS) [*R*], 7 mi. W of Baker, 4600 ft, 2–3 July 1967 (♂), 4♀. — Washington Gulch [*R*], 5 mi. W of Baker, 4000 ft, 2–4 July 1967 (♂). *Benton Co.:* Corvallis [*H*], 13 Sept. 1940, 2♂; 31 Aug. 1951, ♂; 7 Oct. 1952, ♂; ♂. — 9 mi. W of Philomath, 1 Sept. 1949, ♂. *Coos Co.:* Charleston, 9 Aug. 1941, ♂. *Curry Co.:* 2 mi. N of Brookings, ♀. — Pistol River, 17 Sept. 1956, 2♂. *Douglas Co.:* Yoncalla, 1939, ♂. *Jackson Co.:* Ashland, Lithia Park, ♀. — Crater Creek [*M*], 4500 ft, 18–21 Aug. 1950, ♂♀. — Union Creek [*M*], 3300 ft, 1–15 Sept. 1950, 2♂. — Beaver Sulphur Forest Camp near Applegate River, 9 Oct. 1964, ♂. — Siskiyou, 5 July 1951, ♂. *Klamath Co.:* Odell Lake at outlet [*L*], 28 July 1967, 7♂, 5♀. — Willamette Pass Summit, 5130 ft, 17 Aug. 1968, ♂. — Lake of the Woods, 13 Aug. 1935, ♂. — Crater Lake Natl. Pk. [*M*], Headquarters, 21 July 1951, 13 Aug. 1950, 2♂; Sleepy Hollow, 7 Aug. 1950, ♂; Annie Springs, 6000 ft, ♂; ♀. *Lane Co.:* Alderwood St. Pk. [*I*], 200 ft, 29 July 1967, ♂ (♂), 8♀. — Black Canyon Camp (USFS) at SE end of Lookout Point Reservoir [*K*], 29 July 1967, 5♂. — Eugene [*J*], Sept. 1941, 4♂; 12 Aug. 1941, 2♂; 2–23 Nov. 1941, ♂. *Linn Co.:* House Rock Camp, 13 mi. E of Cascadia, 23 July 1949, ♂. *Marion Co.:* Silver Creek Falls, 27 Sept. 1959, ♂. *Multnomah Co.:* Portland [G], 9 Sept. 1947, 2♂; June 1948, ♂; 3 Oct. 1948, ♂; 20 Sept. 1935, ♂; 31 Aug. 1935, ♂; Summer 1934, ♂; Sept. 1934, ♂; 2♂. *Tillamook Co.:* Tillamook, summer 1933, ♂. — Bay Ocean, 3 Sept. 1932, ♂. *Umatilla Co.:* Bear Wallow Camp (USFS) [S], 10 mi. NE of

Ukiah, 4000 ft, 7 July 1967 (2♂), 5♀. — Emigrant Springs St. Pk. [*U*], 3900 ft, 8♀. — 3 mi. NE of Gibbon at Umatilla River [*V*], 1800 ft, 7 July 1967, ♂, ♀. *Union Co.:* 4–5 mi. W of Cove [*T*], 4600 ft, 5 July 1967 (2♂), 2♀. — Catherine Creek St. Pk., 3600 ft, ♀. *Yamhill Co.:* McMinnville, Aug. 1930, fall 1934, 2♂, ♀. WASHINGTON. *Clallam Co.:* Olympic Natl. Pk., Olympic Hot Springs [*C*], 27 July 1968, ♂; 8 Aug. 1968, 2♂. — Crescent Lake [*C*], 10 Sept. 1965, ♂. *Grays Harbor Co.:* Quinalt [*C*], 21 July 1952, ♂, ♀. *Jefferson Co.:* Olympic Natl. Pk., Ho River, Jackson Forest Camp [*C*], 19 Aug. 1956, ♂. *King Co.:* Seattle [*E*], Oct. 1951, ♂; 3 and 12 Sept. 1934, 2♂; 2♂, ♀. *Lewis Co.:* Chehalis, ♀. — Packwood Lake, 11 Aug. 1931, ♂. *Pacific Co.* [*F*]: 1952, 3♂. — Ocean Park, 11 Sept. 1929, 2♂. — Bay Center, 1 Sept. 1933, Aug. 1931, 2♂. — Nahcotta, 20 Aug. 1954, 2♂. *Pierce Co.:* Puyallup, 1931, ♂. — Mt. Ranier Natl. Pk., Longmire, 2000 ft, 1 July 1934, ♂. *San Juan Co.:* Blakeley Island, ♀. — Browns Island, ♀. — Friday Harbor, 2 Aug. 1927, ♂; 20 July 1935, ♂. *Snokomish Co.:* Chase Lake [*D*], 25 Sept. 1954, ♂; June 1956, 4♂. *Thurston Co.:* Olympia, 26 Aug. 1959, ♂; 2♀. *Walla Walla Co.:* Walla Walla [*W*], Nov., ♂; Oct. 1926, 4♂; 10 Oct. 1927, 2♂.

Antrodiaetus occultus new species

Figures 123, 178, 204–206, 248–249.
Map 2.

Type specimens. Holotype male from Corvallis, Linn Co., Oregon, 7 October 1951 (V. Roth), in the American Museum of Natural History. Seven males from type locality with same date designated as paratypes and deposited in AMNH and MCZ. The specific name is a Latin adjective meaning "hidden."

Description. See Tables 12, 13, and 15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype. Females of this species, if present in the material which I have examined, were not distinct enough for me to separate from *A. pacificus* females and therefore remain undescribed.

Male. Carapace: Figure 123. Setae scattered sparsely over pars thoracica except denser along lateral border. *Chelicerae:* Large area on upper ectal surface without setae. *Pedipalps:* Figures 178, 204–206. Tibia strongly swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus roundly pointed; not closely appressed to i.c.s. but bent away from it. Tip of i.c.s. rather well sclerotized and curved (often rather strongly). *Leg I:* Figures 248, 249. Dense group of macrosetae (over 1/3 are ensiform) occupying most of distal 2/3 of prolateral surface of tibia. Small number of scattered macrosetae (usually most attenuate) on retrolateral aspect of ventral surface of tibia; distalmost macroseta not over 3/4 (usually less) of distance from proximal to distal end of tibia. Rarely any macrosetae on ventral surface between these two groups. Tibia thick; swollen at proximal macrosetae group. No macrosetae on metatarsus. Metatarsus sinuous in ventral view. *Abdomen:* 3 dorsal noncontinuous heavily sclerotized patches (sometimes nearly continuous); posterior patch smallest. *Coloration:* Carapace gray-orange or light brown. Labium similar to carapace; sternum and pedipalpal coxae lighter gray-yellow. Chelicerae usually slightly lighter than, sometimes similar to, carapace. Patella, tibia, and metatarsus of leg I medium to dark red-brown; femur lighter but slightly darker than carapace. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale gray-yellow laterally; dorsally posterior of sclerotized patches pigmented light to rather dark gray-brown in dense chevron pattern; sclerotized patches similar to carapace.

Diagnosis. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 248, 249; Table 12) are distinctive for this species. The numerous ensiform macrosetae in the prolateral macrosetae group of the tibia (and often the more proximal position of the distalmost macroseta on the retrolateral aspect of the ventral tibial surface) allow clear separation of *A. occultus* from *A. pacificus*. Since metatarsus I of *A. occultus* is proportionately short, IML/CL, IFL/IML, and ITL/IML (Figs. 248, 249; Table 13) distinguish this species from *A. pacificus* (Fig. 94) and several other *unicolor* group species. The pedipalpal tibia of *A. occultus* is markedly more swollen than in many other *unicolor* group species so that PTT/PTL and PTT/CL (Figs. 96, 178; Table 13) are also excellent diagnostic ratios. Its proportionately large AME's (AMD/CL and AMD/AMS, Table 13; Fig. 123) separate *A. occultus* from several *unicolor* group species. The flexion of the o.c.s. tip away from the i.c.s. (Fig. 204) is a particularly distinctive feature not found in *A. pacificus* and some other species.

Variation. The variation in all characters studied is continuous and usually not wide. Figures 205 and 206 illustrate most of the range of variation observed in o.c.s. tip shape.

Distribution. Western Oregon in the valley between the Coast and Cascade mountain ranges (Map 2).

Records. OREGON. *Benton Co.:* Corvallis, 7 Oct. 1951, 8♂; 7–9 Oct. 1912, 3♂; 8 Nov. 1895, ♂; winter 1936, ♂; 10 Oct. 1947, ♂; 21 Oct. 1934, ♂. *Clackamas Co.:* 3 mi. N of Marguam, 26 Sept. 1964, ♂. — Oregon City, 30 Sept. 1950, ♂. *Douglas Co.:* Roseburg, 22 Sept. 1946, ♂. — Yoncalla, 1939, ♂. *Lane Co.:* Eugene, Oct. 1927, ♂; 12 Oct. 1941, ♂.

Antrodiaetus pugnax (Chamberlin)

Figures 109–112, 124, 132, 161, 179, 207–212, 250–252, 292–294. Map 2.

Brachybothrium pugnax Chamberlin, 1917, Bull. Mus. Comp. Zool., 61(3): 73. Holotype collected by Charles Bendire; in the Museum of Comparative Zoology; examined. (See comments below on sex of holotype and designated type locality.) –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 907.

Brachybothrium shoshoneum Chamberlin, 1925, Proc. California Acad. Sci., 14(7): 105, figs. 1–3. Holotype male from Troy, Latah Co., Idaho, 16 August 1908; in the Museum of Comparative Zoology; examined. NEW SYNONYMY. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 907.

Comments on original description. The holotype of *Brachybothrium pugnax* is clearly a mosaic gynandromorph with at least some intersexual tissue, but has enough diagnostic male structures to show its conspecificity with the holotype male of *B. shoshoneum*. Although Chamberlin (1917) described the abnormal right pedipalp and the differences between the holotype chelicerae, he did not state that the specimen was gynandromorphic or teratological. Such a description published even today would not violate Article 1 of the present International Code of Zoological Nomenclature (1964) which states that "names given . . . to teratological specimens . . . as such . . . are excluded" from the Code.

There is considerable evidence to indicate that the type locality which Chamberlin designated for *A. pugnax*—Tucson, Arizona—is in error. All other records for this species are clustered in the Pacific Northwest (Map 2) over 1100 air miles from Tucson, even though numerous specimens of other antrodiaetid species have been collected from the intervening area. Both labels accompanying the holotype are in Chamberlin's handwriting. The stated locality, written on both pieces of paper, reads "Arizona: Tucson (Bendier coll.)" and "Tucson, Ariz. Bendier coll." Chamberlin's handwriting and the misspelling of the collector's (Charles Bendire) name indicate that this information was transferred from some source. Errors may have been present in the source and/or committed during the transfer. (The type localities of five of the 34 new species described by Chamberlin in the same publication were either unknown or followed by a question mark.)

Charles Bendire, who collected the specimen, was a U. S. Army officer and prominent naturalist who collected and gave, chiefly to the U. S. National Museum, large quantities of natural history specimens (primarily bird eggs, birds, and other vertebrates) from the western U. S. (Merriam, 1897; Merrill, 1898; Mearns, 1902). Not until about 1870, while stationed in Idaho, did he begin collecting large numbers of specimens (Merrill, 1898). While earnestly collecting in the West (1870–1886), he was stationed in Oregon, Washington, and Idaho for about 10.5 years, in Arizona for only 1.5 years, and elsewhere about 4 years (Merrill, 1898). He therefore spent the great majority of his collecting time within or near the Pacific Northwest distribution range of *A. pugnax*. In summary, the evidence suggests both an error in the designation of the type locality and that the real type locality is somewhere in Oregon, Washington, or Idaho.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Holotype. Since the holotype of *A. pugnax* is a mosaic gynandromorph with some portions of the body also exhibiting intersexuality, it is not included in the species population sample for which quantitative character values are summarized in Tables 12–14, but its measurements are given in Table 15. The holotype is larger than other known *A. pugnax* males and females except for one somewhat shrivelled and unmeasured male lacking a locality label. The left chelicera of the holotype is composed of male tissue; it is small, possesses a typical anterior-dorsal protuberance, and lacks a rastellum. The highly diagnostic tibia and metatarsus of the left leg I, which is also composed of male tissue, match those of males from the eastern portion of the species range. (The other leg I and the left pedipalp are missing.) At least much of the abdomen, with a male genital opening and 3 heavily sclerotized patches dorsally, is composed of male tissue, but the EGS are abnormally numerous (Table 15). The sole demonstrable female structure is the right chelicera, which is much larger than the left one, lacks a male protuberance, and possesses a well-developed rastellum. Possibly a substantial part of the cephalothorax is also female tissue. The right pedipalp is intersexual. Its tibia is partially swollen and possesses some (but fewer than the normal female complement of) ensiform macrosetae. The tarsus is also swollen, possesses some ensiform macrosetae, is somewhat hollowed out ventrally on the distal half, and the claw is slightly enlarged and partly sheathed in a rudimentary o.c.s. At least some of the legs and possibly much of the cephalothorax also contain intersexual tissue.

Male. Carapace: Figures 109, 124. Setae sparse to moderately dense on pars thoracica; always moderately dense along lateral border. *Chelicerae:* Usually a large to small setaless area on upper ectal surface; occasionally setae cover entire upper ectal surface. *Pedipalps:* Figures 179, 207–212. Tibia moderately swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus pointed and closely appressed to i.c.s. I.c.s. tip well sclerotized (occasionally side against o.c.s. nearly translucent) and straight or only weakly curved. *Leg I:* Figures 101, 250–252. Dense group of macrosetae (majority ensiform) on prolateral surface of tibia, centered just distal of midpoint. Another smaller group of macrosetae (50% or more are ensiform) on retrolateral aspect of ventral surface of tibia; distalmost macroseta positioned at 2/3 or less of distance from proximal to distal end; distalmost macrosetae of this group very large. No macrosetae between these groups. Tibia swollen at ventral macrosetae group. One to 4 macrosetae ventrally at distal end of metatarsus; occasionally a macroseta also positioned ventrally at 2/3 distance from proximal to distal end. Metatarsus with keellike swelling on retrolateral aspect of ventral surface at between 1/3 to 1/2 of distance from proximal to distal end; weakly sinuous in ventral view. *Abdomen:* 3 (occasionally 2) frequently continuous, dorsal, heavily sclerotized patches; third (posterior) patch varies from absent to nearly as large as others. *Coloration:* Carapace pale gray-yellow to gray-orange. Sternum and pedipalpal coxae paler gray-yellow; labium yellow-gray. Chelicerae similar to carapace, often slightly lighter. Patella, tibia and metatarsus of leg I orange to red-brown; femur lighter. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray to gray-brown; usually darkest pigment dorsally and lighter laterally; dorsal sclerotized patches gray-yellow to gray-brown, usually darker than rest of abdomen.

Female. Carapace: Figures 110, 132. Setae density on pars thoracica as in male. *Chelicerae:* Figure 161. Microteeth positioned beside last 5 to last 2 macroteeth and often extend beyond last macrotooth. Microteeth small to medium in size. Setae sometimes scattered over entire upper ectal surface, sometimes absent from small to large part of this surface. *Abdomen:* Background setae on dorsum moderately slender and distributed moderately densely. *Genitalia:* Figures 292–294. Seminal receptacles with well-sclerotized stalk and bowl; usually of moderate length and breadth. Stalk frequently expanded basally. Bowl usually well developed; its border with bulb sharply defined. Floor of bursa copulatrix weakly to moderately well sclerotized. *Coloration:* Carapace gray-yellow to light brown; pars cephalica frequently slightly darker than pars thoracica. Sternum similar to pars thoracica; labium and pedipalpal coxae darker than carapace. Chelicerae light brown to brown, markedly darker than carapace. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen pale gray-yellow, sometimes with darker gray-brown pigmentation dorsally; tergite similar to pars thoracica.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 101, 250–252; Table 12) are distinctive for this species and include the best characters for identification. Because of the proportionately long tarsus I and a proportionately shorter metatarsus I than in some species. IML/ITarL, ITL/ITarL, ITL/IML, and occasionally other ratios (Table 13) separate *A. pugnax* from several *unicolor* group species, particularly *A. pacificus.* ITL, IFL, PFL, and other measurements (Table 13) help separate *A. pugnax* with its small mean body size from the larger species *A. hageni* and *A. montanus. Females. A. pugnax* has a significantly smaller mean body size than most other *unicolor* group species; many appendage and carapace measurements (Table 14) are diagnostically useful, giving particularly good separation from the large sympatric species, *A. hageni* and *A. montanus.* As a result of the proportionately long tarsus IV and other leg IV segments that are relatively short, IVML/IVTarL and IVTL/ IVTarL (Table 14) help distinguish *A. pugnax* from *A. hageni* and *A. cerberus.* The best ratio for separating *A. pugnax* from *A. pacificus* is IVML/IML, and from *A. montanus* is IFL/IML (Table 14). The small cheliceral microteeth (Fig. 161) of *A. pugnax* help distinguish this species from both *A. hageni* and *A. montanus.*

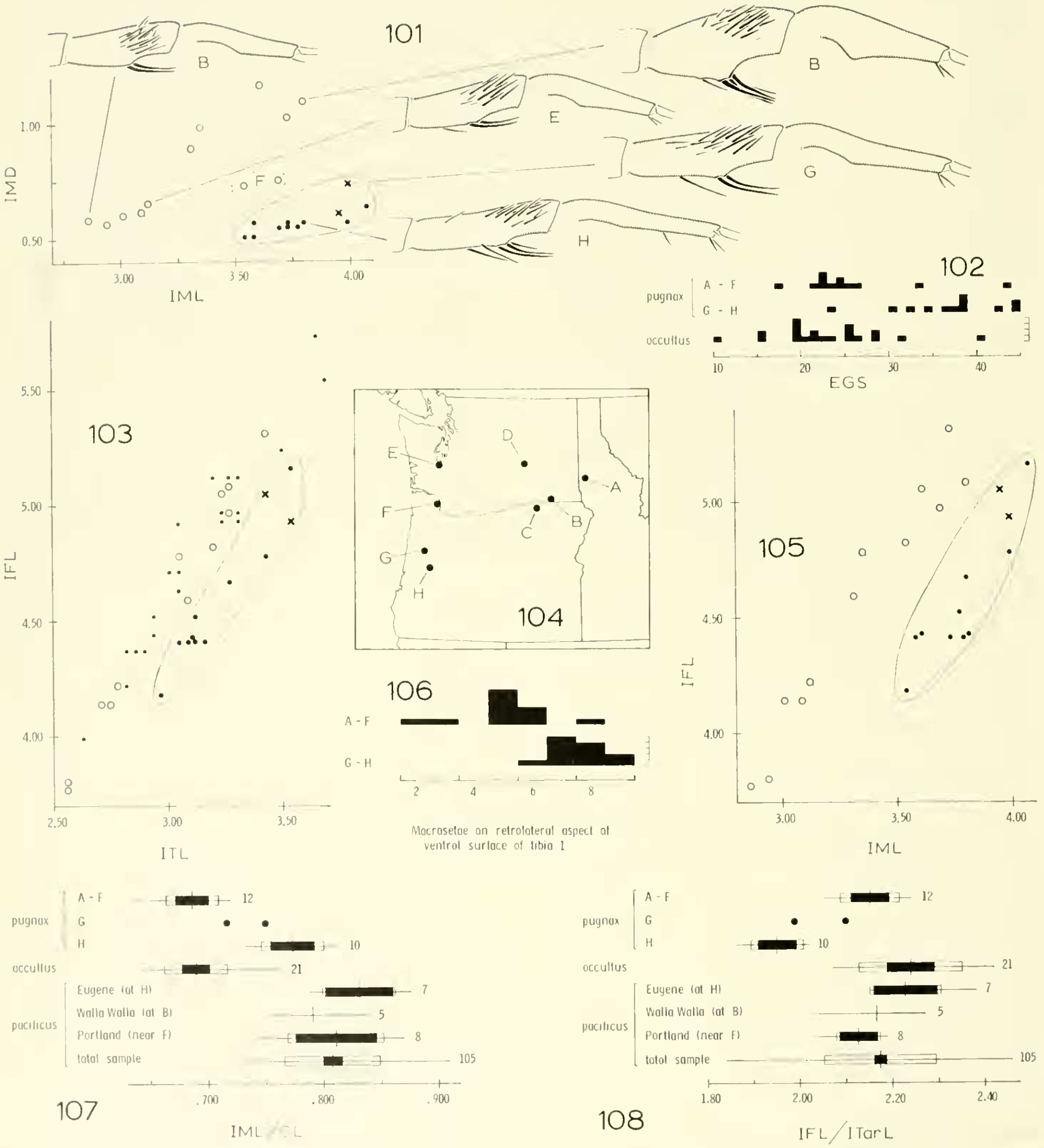
Variation. A number of characters exhibit strong geographic variation in male *A. pugnax.* On the other hand, comparisons of four female samples (from Corvallis, Ore., and from Ft. Lewis, Walla Walla, and Lewis and Clark St. Park, Wash.) reveal no marked geographic variation. Male quantitative characters with the strongest geographic variation are (in approximate order of the degree of discontinuity of variation): IFL/IML, IFL/ITL, IML/CL, IFL/ITarL, IMD/IML, ITD/ITL, metatarsus I macrosetae number, tibia I macrosetae number, EGS, and ALD/CL.

For the first four of these characters, population sample *H* is distinct from the northern and eastern samples, which have a proportionately shorter leg I tibia, metatarsus, and tarsus (Figs. 103–108). Sample *G* is similar in these characters to sample *H* or is intermediate. The geographic patterns of IMD/IML (Fig. 101) and ITD/ITL variation are very similar to each other and resemble those of the above characters. However, this variation appears somewhat clinal, with sample *F* intermediate. The thickest tibiae and metatarsi I (also with the most prominent protuberances) are in the northeastern part of the species range and are the most slender in the southwestern portion (Fig. 101). All sample *H* specimens have on metatarsus I a macroseta F (Fig. 252), not present on other males except the one from *A*. Also there is a much greater tendency for sample *H* individuals to have metatarsal macrosetae C and D (Fig. 252) and for macroseta B to be ensiform. The southwestern samples (*G*, *H*) have a significantly higher mean number of EGS (Fig. 102) and of macrosetae on the retrolateral aspect of the ventral surface of tibia I (Fig. 106) than northern and eastern samples. ALD/CL exhibits a different pattern of geographic variation, with samples *E* and *F* having markedly smaller mean values of this character than samples *B* and *H*, but only small gaps separate the variation ranges of these small samples.

Clearly population *H* is genetically divergent and could be satisfactorily distinguished from the known northern and eastern samples by most of the above (male) characters. However, present evidence does not justify concluding that population *H* is reproductively isolated from the rest. Geographically intermediate and larger samples need to be studied. The intermediate position of sample *G* and (occasionally) sample *F* in the variation pattern of some markedly varying characters is some evidence that populations *H* and *G* are exchanging genes, but perhaps at a reduced rate, with the more northerly known populations. Perhaps favorable *A. pugnax* habitat is discontinuous in the Willamette River Valley area of northwestern Oregon, thus hindering gene exchange with northern and eastern populations. Another factor possibly involved is character divergence.

It seems highly unlikely that character divergence between *A. pugnax* and *A. pacificus* could cause such geographic variation in *A. pugnax*, since *A. pugnax* is throughout its entire range sympatric with *A. pacificus* (Map 2), unless possibly an uncommon situation of strong local competition exists between *A. pacificus* and semi-isolated *A. pugnax* populations only in the Eugene, Oregon, area (samples *G* and *H*) where their habitats are spatially intermingled. An examination of all characters for variation patterns that could result from such character divergence reveals that 1/6 do have such a variation pattern (one in which the *A. pugnax* population samples *G* and *H* are markedly more distinct from the Eugene [sympatric] *A. pacificus* sample than are the other *A. pugnax* samples). But almost as many characters had just the opposite pattern. IFL/ITarL, ITarL/CL, PFL/CL, and IFL/ITL show the former type of pattern most strongly (Fig. 108), whereas IML/CL, ITL/ITarL, and IFL/IML exhibit the strongest reverse pattern (Fig. 107).

There is considerable evidence, however, to suggest character divergence between *A. pugnax* and *A. occultus*. Records indicate that *A. occultus* is found only in the Willamette River Valley region, where it is sympatric with *A. pugnax* (Map 2). Both species have been collected from



Figures 101–108. Geographic variation in *Antradiaetus pugnax* males. (All measurements in mm. For scatter diagrams large black dots represent sample *H*, x's sample G, and circles samples *A–F*.) 101. Scatter diagram of IMD and IML. 102. Histogram of EGS number compared with that of *Antradiaetus occultus.* (One unit of vertical scale represents one specimen.) 103. Scatter diagram of IFL and ITL. (Small black dots represent *A. occultus* males.) 104. Map of population sample localities. 105. Scatter diagram of IFL and IML. 106. Histogram of tibia I retrolateral-ventral macrosetae number . (One unit of vertical scale represents one tibia.) 107. Mod. Dice-Leraas diagram of IML/CL variation compared with that of *A. occultus* and *Antradiaetus pacificus.* 108. Mod. Dice-Leraas diagram of IFL/ITarL variation compared with that of *A. occultus* and *A. pacificus.*

Eugene and Corvallis, Oregon. Unfortunately, the habitat of *A. occultus* is unknown. Of 43 quantitative characters examined, the sympatric population sample of *A. pugnax* is markedly more distinct from *A. occultus* than are the allopatric *A. pugnax* population samples—the pattern that could be the result of character displacement—in 20 of these characters, whereas only five characters show the opposite pattern. IML/CL, IFL/ITL, CW/CL, and IFL/ITarL are the best examples of the former pattern (Figs. 103, 107, 108); ITL/IML yields the most strongly expressed reverse pattern.

Noteworthy variation, usually with a geographic pattern similar to the dominant one shown by quantitative characters, are shown by a number of not strictly quantitatively defined characters. *Males:* Three specimens from *B* and *C* have only a tiny area devoid of setae on the upper ectal surface of the chelicerae, while the rest in the species sample have larger setaless areas, the largest being from the westernmost localities. There is considerable variation (but without a clear geographic pattern) in the shape of the i.c.s. tip and in the distance that it extends beyond the o.c.s. tip (Figs. 207, 209, 211). The o.c.s. tip is also quite variable in shape and averages wider and shorter in sample *H* (Figs. 208, 210, 212). The basal portion of the palpus is larger relative to the length of the conductor portion in most southwestern specimens (Figs. 207, 209). While specimens from the eastern part of the species range have either only two or three noncontinuous, heavily sclerotized patches on their abdominal dorsum, western specimens have three usually continuous patches. *Females:* Most specimens from *B* have the upper ectal surface of their chelicerae evenly covered with setae, the rest of the eastern specimens have here a small to medium size setaless area, and in western specimens this area is large. The seminal receptacle stalks are usually proportionately much longer and the stalk bases less expanded in eastern than in western specimens (Figs. 292–294). Occasionally a part of the anterior edge of the bursa copulatrix floor is very heavily sclerotized (Fig. 294).

Distribution. Northern Oregon, southern Washington, into northwestern Idaho (Map 2).

Records. IDAHO. *Latah Co.:* Troy [*A*], 16 Aug. 1908, ♂. OREGON. *Benton Co.:* Corvallis [*G*], 18 Aug. 1949, ♂; 3♀. — McDonald Forest [*G*], 3/4 mi. E of saddle, 10 Aug. 1962, ♂. *Columbia Co.:* St. Helens [*F*], 2 Aug. 1934, ♂; 6 Aug. 1936, ♂. *Lane Co.:* Eugene [*H*], Sept. 1941, 11♂. *Umatilla Co.:* Pendleton [C], ♂. *Union Co.:* Fly Creek Valley, S of Starkey, ♀. WASHINGTON. *Columbia Co.:* Lewis and Clark Trail St. Pk., 1000 ft, 4♀. *Grant Co.:* Larson Air Force Base [*D*], 10 Oct. 1958, ♂. *Pierce Co.:* Fort Lewis, 2♀. *Thurston Co.:* Olympia [*E*], winter 1939, ♂; 26 Aug. 1959, ♂; ♂, 2♀. *Walla Walla Co.:* W edge of Walla Walla [*B*], 930 ft, 8–9 July 1967, 2(♂), 11♀. — Walla Walla [*B*], 10 Sept. 1927, ♂; Oct. 1926, ♂. *Yakima Co.:* Tieton, ♀.

Antrodiaetus montanus (Chamberlin and Ivie)

Figures 140, 150, 162, 171, 180, 213–217, 253–255, 295–298. Map 2.

Brachybothrium hageni: Chamberlin and Ivie (not Chamberlin, 1917), 1933, Bull. Univ. Utah, 23(4): 4.

Brachybothrium montanum Chamberlin and Ivie, 1935, Bull. Univ. Utah, 26(4): 4, pl. 5, fig. 31. Holotype male and allotype female from 8 miles S of Lynn, Raft River Mountains, Box Elder Co., Utah, 6 Sept. 1932; in the American Museum of Natural History; examined. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 907.

Antrodiaetus montanus: Chamberlin and Ivie, 1945, Ann. Ent. Soc. America, 38(4): 549, pl. 1, figs. 1–2.

Antrodiaetus hageni: Bonnet (in part), 1955, Bibliographia Araneorum, 2: 335.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Setation usually rather dense on lateral border, particularly posteriorly. *Chelicerae:* Figure 150. Upper ectal surface covered with scattered setae. *Pedipalps:* Figures 180, 213–217. Tibia moderately swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. O.c.s. of palpus slightly widened distally; tip weakly pointed to blunt, usually not closely appressed to i.c.s. I.c.s. tip well sclerotized and curved (often strongly). *Leg I:* Figures 253–255. Rather large dense group of macrosetae (most are ensiform) on distal 1/2 to 2/3 of prolateral surface of tibia. Smaller group of more scattered macrosetae (1/3 or more are ensiform) centered more proximally at 1/2 to 2/3 of distance from proximal to distal end of tibia on ventral aspect of retrolateral surface. These groups clearly separated by ventral area lacking macrosetae. Prolateral portion of distal half of tibia swollen. Usually 1 (very rarely more) and sometimes no macrosetae ventrally at distal end of metatarsus. Metatarsus weakly sinuous in ventral view. *Abdomen:* 3 dorsal, heavily sclerotized, usually noncontinuous patches. Posterior patch usually smallest, sometimes reduced to bilateral pair of small patches. *Coloration:* Carapace pale gray-yellow to pale gray-orange. Sternum paler; labium darker yellow-gray or orange-gray. Chelicerae similar to carapace. Patella, tibia, and metatarsus of leg I often light to medium orange, darker than carapace; femur lighter. Pedipalps and other legs, sometimes also leg I, dorsally similar to carapace, ventrally lighter. Abdomen pale gray-yellow to light gray; dorsal sclerotized patches often slightly darker gray-yellow or gray-orange.

Female. Carapace: Setae sparsely scattered over much of pars thoracica, especially dense along lateral border. *Sternum:* Figure 140. Relatively broad. *Chelicerae:* Figures 162, 171. Microteeth positioned beside last 8 to last 5 macroteeth, sometimes extending beyond last macrotooth. Outermost microteeth usually very large. Entire upper ectal surface covered with scattered setae. *Abdomen:* Background setae on dorsum rather short, slender, and distributed densely. *Genitalia:* Figures 295–298. Seminal receptacles with well-sclerotized stalk and bowl; of moderate length and breadth. Stalk slightly expanded at its base and constricted above. Bowl well developed; its border with bulb sharply defined. Floor of bursa copulatrix rather well sclerotized. *Coloration:* Carapace pale to medium gray-yellow; pars cephalica sometimes slightly darker than pars thoracica. Sternum similar to pars thoracica; pedipalpal coxae and especially labium darker light gray-orange to light brown. Chelicerae light gray-orange to light orange-brown, darker than carapace. Pedipalps and legs dorsally similar to or slightly darker than carapace, ventrally lighter. Abdomen yellow-gray or gray; tergite usually darker gray-yellow or light brown.

Diagnosis. The presence of setae over the entire upper ectal surface of the chelicerae (Fig. 171) and the light coloration help separate both sexes of *A. montanus* from *A. pacificus*, *A. cerberus*, and some other *unicolor* group species and are especially important for female identifications. *Males.* The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 253–255; Table 12) are distinctive for this species. Because the femur, tibia, and tarsus of leg I are relatively longer in *A. montanus* than in other *unicolor* group species, ITL/CL, ITarL/CL, and other ratios involving these segment lengths (Table 13) are usually excellent characters for identification. ITL/IML (Table 13) is the character that most accurately separates *A. montanus* from the similar species, *A. pacificus*. *A. montanus* has a relatively long pedipalpal femur, making PFL/CL (Table 13) a useful ratio for separating this species from *A. cerberus* and a few other *unicolor* group species.

Females. The color and setation characters mentioned above are quite useful. Some raw measurements (particularly IVTL and IVML, Table 14) help separate *A. montanus,* with its large body size, from *A. pugnax* and *A. pacificus.* Individuals of this species usually have a higher CMT number (Table 14) and larger microteeth (Fig. 162) than those of other *unicolor* group species. The expanded seminal receptacle stalk bases (Figs. 295–298), apparently characteristic of this species, have not been found in any specimens of *A. hageni* or *A. cerberus.*

Variation. Males: No characters studied exhibit either discontinuous variation or marked geographic variation. Macroseta A on metatarsus I usually varies from large and ensiform to small and attenuate, but is occasionally reduced to a normal seta (Table 12). There is rather wide but continuous variation in the number of macrosetae (total and ensiform) and proportion of ensiform macrosetae in the tibia I macrosetae groups (Table 12; Figs. 253, 255). Specimens from Crater Lake and Fish Lake, Oregon, have the highest numbers of macrosetae in the prolateral group. Noteworthy variation is found in the thickness and rate of taper of the tip of the i.c.s. of the palpus. Figures 213 and 215 illustrate most of the variation range of this character. Figures 214–217 illustrate much of the variation range in o.c.s. tip shape and width. The size of the posterior (third) sclerotized patch on the abdominal dorsum varies greatly, from almost as large as the other patches to a pair of tiny, bilaterally arranged patches.

Females: Few characters exhibit marked variation. The considerable variation in the ratio of stalk diameter to bowl diameter of the seminal receptacles is illustrated in Figures 295–298. The smaller (perhaps younger) adult females often have relatively wider stalks and less well-defined bowls than larger females. In two of the larger specimens the seminal receptacle bowls are rather well sclerotized. Although most individuals have a high CMT number and cheliceral microteeth of large size (Fig. 162), one adult female (included in the species sample) from Crater Lake, Oregon, and a large immature female from Fish Lake, Oregon, are at the low end of the CMT number range (Table 14) and have relatively much smaller cheliceral microteeth than do the rest of the specimens.

Specimens of uncertain identity. There are a few geographically scattered adult female specimens and two larger samples of females, which, although they are similar to *A. montanus* in most characters (including most diagnostic characters), have not been included in the species sample because, in addition to being from localities where *A. hageni* and *A. pacificus* are sympatric with *A. montanus,* they also agree more closely with *A. hageni* or *A. pacificus* in some of the characters diagnostic for the *A. montanus* sample. Two adult females composing one such sample from Pendleton, Oregon, have smaller *A. hageni*-like cheliceral microteeth and seminal receptacle stalks shaped like those of *A. hageni,* and are clearly intermediate in other characters, including the normally diagnostic ratio SL/SW. The other such sample of three adult females, from Manzanita Lake (Shasta Co.), California, is similar to *A. pacificus* in CMT number and cheliceral microtooth size. If, as is suspected, such specimens prove to be *A. montanus* and not variants of the other species or hybrids, then the diagnostic usefulness for *A. montanus* of CMT number, cheliceral microteeth size and, to a lesser extent, of SL/SW will be reduced.

Distribution. Chiefly the Great Basin region from Utah and Nevada north to Washington (Map 2).

Records. IDAHO. *Ada Co.:* near Boise, Cottonwood Gulch, 2 Nov. 1919, ♂. *Bannock Co.:* 7 mi. S of Downey, 5200 ft, ♀. — 1 mi. E of Pocatello in Pocatello Creek

Valley, 3♀. *Bonneville Co.:* Idaho Falls, Aug. 1966, ♂. *Canyon Co.:* Notus, Oct. 1932, ♂. *Latah Co.:* Moscow, 4 Nov. 1964, ♂. *Power Co.:* American Falls, 28 Sept. 1962, ♂. NEVADA. *Elko Co.:* Elko, ♂, ♀. *Washoe Co.:* Reno, ♀. — Washoe Valley, 11 Oct. 1967, ♂. — Verdi, 9 Oct. 1967, ♂. OREGON. *Harney Co.:* Steens Mtns., Fish Lake, 7200 ft, 16 Aug. 1958, ♂, ♀. *Klamath Co.:* Crater L. Nat'l Pk., Annie Springs, 6000 ft, 6–7 Aug. 1959, 2♂; ♀. UTAH. 8 Oct. 1927, ♂. *Box Elder Co.:* Raft R. Mtns., 8 mi. S of Lynn, 6 Sept. 1932, ♂, ♀. *Salt Lake Co.:* Little Cottonwood Canyon, Aug. 1900, ♂. — vicinity of Salt Lake City, Oct. 1927–1931, 4♂. — Salt Lake City, 21 Aug. 1931, ♂; 1929, ♂; 2♀. — Salt Lake City at Fort Douglas, 22 Oct. 1932, ♂. — Mouth of City Creek Canyon near Salt Lake City, ♀. — Mill Creek Canyon, 2♀. *Summit Co.:* N Fork Provo R. at Cobble Rest, 23 Sept. 1932, 3♂. *Utah Co.:* W side Utah Lake, ♀. *Wasatch Co.:* Strawberry Reservoir, Oct. 1928, ♂. WYOMING. *Lincoln Co.:* Cokeville, Aug. 1931, ♂.

Antrodiaetus hageni (Chamberlin)

Figures 125, 133, 141, 151, 163, 172, 181, 218–219, 256–257, 299–300. Map 2.

Brachybothrium hageni Chamberlin, 1917, Bull. Mus. Comp. Zool., 61(3): 74, pl. 5, fig. 9. Holotype male from Loon Lake, Stevens Co., Washington, 25 July 1882; in the Museum of Comparative Zoology; examined. –Roewer, 1942, Katalog der Araneae, 1: 190.

Antrodiaetus hageni: Bonnet (in part), 1955, Bibliographia Araneorum, 2: 335. –Thorn, 1967, British Columbia Prov. Mus. Annual Report, p. 1. (*Antrodiaetes*).

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Figure 125. Setae numerous over most of pars thoracica, particularly dense along lateral border. *Chelicerae:* Figure 151. Entire upper ectal surface covered with scattered setae. *Pedipalps:* Figures 181, 218, 219. Tibia moderately swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus pointed (profile knifelike) and closely appressed to i.c.s. I.c.s. somewhat widened; tip well sclerotized and only weakly curved. *Leg I:* Figures 256, 257. Large dense group of macrosetae (nearly all ensiform) on prolateral surface of middle 1/3 of tibia. Another smaller group of macrosetae (great majority ensiform) on ventral aspect of retrolateral surface of distal 1/2 of tibia. Usually a few macrosetae on ventral surface between these two groups. Tibia weakly bowed laterally so that prolateral surface convex. One to 3 macrosetae (rarely none) ventrally at distal end of metatarsus. Metatarsus with thick, strong, retrolaterally and ventrally produced elbow just proximal of midpoint. *Abdomen:* 3 dorsal, heavily sclerotized, noncontinuous patches, occasionally with a fourth area of tiny sclerotized spots at bases of 2 to 4 large, transversely arranged setae. Anterior patch largest; second patch next largest. *Coloration:* (The holotype probably darkened during the 35 years between its collection and its description by Chamberlin. The following description is based on less discolored specimens.) Carapace pale gray-yellow to pale gray-orange. Sternum paler gray-yellow; labium darker yellow-gray. Chelicerae light yellow to orange-gray, usually darker than carapace. Patella, tibia, and metatarsus of leg I orange to red-brown, femur lighter. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray to light gray; dorsal sclerotized patches usually slightly darker light gray-yellow or gray-orange.

Female. Carapace: Figure 133. Setae cover pars thoracica as in male; quite dense along lateral border. *Sternum:* Figure 141. *Chelicerae:* Figures 163, 172. Microteeth positioned beside last 8 to last 3 macroteeth, except sometimes not extending beyond penultimate macroteeth and sometimes extending beyond last macrotooth. Most microteeth rather large. Entire upper ectal surface covered with scattered setae. *Abdomen:* Dorsal background setae rather short, slender, and distributed densely. *Genitalia:* Figures 299, 300. Seminal receptacles with well-sclerotized stalk and bowl; of moderate length and breath. Stalk not expanded basally. Bowl well developed; its border with bulb sharply defined. Floor of bursa copulatrix rather well sclerotized. *Coloration:* Pars thoracica pale gray-yellow; pars cephalica slightly darker yellow. Sternum similar to pars cephalica; labium and pedipalpal coxae a darker light brown. Chelicerae light to medium brown, much darker than carapace. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen yellow-gray; tergite gray-yellow.

Diagnosis. The light color of the carapace and abdomen, the presence of setae over the entire upper ectal surface of the chelicerae (Fig. 172), and the abundance of setae on the pars thoracica help to separate both sexes of *A. hageni* from *A. pacificus* and *A. cerberus*, and are especially important for female determinations. *Males.* The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 256, 257; Table 12) are distinctive for this species, and include the best characters for identification. Ratios expressing the relative lengths of leg I segments, particularly the proportionately short metatarsus, help separate *A. hageni* from some of the other *unicolor* group species (See ITL/IML, IML/CL, and ITL/CL; Table 13.). AMD/CL (Table 13) helps separate this species, with its relatively small AME's, from several others possessing large eyes. Because of its especially large pedipalp, PTL and PFL (Table 13) distinguish *A. hageni* from *A. yesoensis*, *A. pugnax*, and *A. cerberus*. The pointed knifelike profile of the o.c.s. tip is not found in several other *unicolor* group species.

Females. The color and setation characters mentioned above are diagnostically quite helpful. The following characters are the most useful in separating *A. hageni* from the similar species, *A. montanus:* 1) Seminal receptacle stalks not expanded basally (Figs. 299, 300). 2) Sternum usually narrower (Fig. 141; SL/SW, Table 14). 3) Usually fewer cheliceral microteeth (CMT, Table 14), and these average slightly smaller (Fig. 163). 4) ALE's usually larger and closer together (Fig. 133; ALS/ALD, Table 14).

Variation. Variation within the available species sample for each sex is not markedly large or discontinuous for nearly all characters studied. *Males:* Noteworthy variation is found (Table 12) in the metatarsus I macrosetae arrangement and in the total number of macrosetae in the prolateral group on tibia I; however, the percent of ensiform macrosetae in this latter group has a small range of variation. Although usually separated, the two tibia I macrosetae groups are essentially continuous on the specimen (Baker, Oregon) with the highest tibia I macrosetae number. Tibia I and particularly metatarsus I of most specimens are more slender than those of the holotype (Fig. 256). *Females:* Figures 299 and 300 are representative of the small amount of variation found in seminal receptacle shape and arrangement.

Distribution. South central British Columbia, eastern Washington, and eastern Oregon (Map 2).

Records. BRITISH COLUMBIA. Trail, 23 Oct. 1934, ♂. — E edge of Trail, 1500 ft, 13 July 1967 (♂), 2♀. — Summerland, 15 Aug. 1925, ♂. —Vernon, ♂. — Kamloops, ♀. — Kelowna, ♀. — Oliver, ♀. — E side Vaseux Lake, near Oliver, 1000 ft, ♀. OREGON. *Baker Co.:* Spring Creek, NW of Baker, 4000 ft, 16 Oct. 1955, ♂; 11–12 Sept. 1960, 2♂. — 1/2 mi. E of Baker, 3500 ft, 2♀. WASHINGTON. *Stevens Co.:* Loon Lake, 25 July 1882, ♂.

Antrodiaetus cerberus new species

Figures 126, 134, 164, 182, 220–221, 258–259, 301–302. Map 2.

Type specimens. Holotype male from Cedar Lake (N of Leadpoint), Stevens Co., Washington, May 1962 (W. Ivie); in the American Museum of Natural History. Three males and 5 females from type locality with same date designated as paratypes and deposited in AMNH and MCZ. The specific name is a noun in apposition after *Cerberus*, the dog of Greek mythology that guards the entrance to Hades.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Figure 126. Few setae on pars thoracica, most of these concentrated along lateral border. *Chelicerae:* Large area on upper ectal surface without setae. *Pedipalps:* Figures 182, 220, 221. Tibia moderately swollen in lateral view; greatest diameter in lateral view at between 1/3 to 1/2 of distance from proximal to distal end, but dorsal and ventral outlines in lateral view nearly parallel except near both ends. Tip of o.c.s. of palpus blunt and closely appressed to i.c.s. Tip of i.c.s. only moderately heavily sclerotized; side against o.c.s. very thin and translucent. *Leg I:* Figures 258, 259. Compact group of relatively elongate and slender macrosetae (over 80% are ensiform) centered at about 2/3 of distance from proximal to distal end of tibia on prolateral surface. Another smaller group of similarly slender macrosetae (over 80% are ensiform) scattered along retrolateral aspect of ventral surface of tibia; distalmost macroseta about 3/4 of distance from proximal to distal end of tibia. One to several slender macrosetae (most ensiform) on ventral surface between these two groups. Tibia swollen prolaterally and ventrally at macrosetae groups. Usually 2 (occasionally 1) macrosetae ventrally at distal end of metatarsus. Metatarsus rather sinuous in ventral view. *Abdomen:* 3 dorsal, heavily sclerotized, usually continuous patches; posterior patch smallest. *Coloration:* Carapace gray-yellow (tan). Sternum and pedipalpal coxae pale yellow; labium darker yellow-gray. Chelicerae similar to carapace. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray dorsally; darker gray ventrally posterior of book lungs. Dorsal sclerotized patches gray-yellow, similar to carapace. Faint dark chevronlike markings on abdominal dorsum behind sclerotized patches.

Female. Carapace: Figure 134. Setae very sparsely scattered over pars thoracica, most along lateral border. *Chelicerae:* Figure 164. Microteeth positioned beside last 7 to last 4 macroteeth and often extend beyond last macrotooth. Largest microteeth moderately large. Most of upper ectal surface of chelicerae, except for patchy small to medium-sized bare area, covered with scattered setae. *Genitalia:* Figures 301, 302. Seminal receptacles with well-sclerotized stalk and bowl; of moderate length and breadth. Stalk not or very slightly expanded basally. Bowl well developed; its border with bulb well defined. Floor of bursa copulatrix quite weakly sclerotized. *Coloration:* Carapace gray-yellow (often a deep tan). Sternum similar or slightly lighter gray-yellow; labium and pedipalpal coxae a darker light brown. Chelicerae brown, markedly darker than carapace. Legs and pedipalps dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray except for dark dorsal area which becomes chevronlike posteriorly; tergite similar to carapace.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 258, 259; Table 12) are distinctive for this species. AMD and ratios involving AMD (Fig. 126; Table 13) are helpful in separating *A. cerberus* from most other *unicolor* group species because of its small AME's. Because of the proportionately short tarsus

I and metatarsus I of this species, ITL/ITarL and other ratios incorporating ITarL and IML are excellent diagnostic characters (Fig. 259; Table 13). Clear separation from *unicolor* group species with strongly swollen pedipalpal tibia is obtained by using PTT and PTT/CL (Fig. 182; Table 13). The partly translucent i.c.s. tip (Fig. 220) is not found in any other sympatric *unicolor* group species. The absence of setae over a large part of the upper ectal surface of the chelicerae allows quick separation from *A. hageni* and *A. montanus.*

Females. As is true for the males, AMD, AMD/CL, and other ratios incorporating AMD are helpful in separating *A. cerberus* females, with their small AME's, from several other *unicolor* group species (Fig. 134; Table 14). *A. cerberus* has a proportionately short tarsus IV and metatarsus I, and a proportionately long tibia IV, metatarsus IV, and femur I, so that the following ratios are the best characters for separating *A. cerberus* from the following sympatric (or nearly sympatric) species: *A. pacificus,* IVML/IML; *A. hageni,* IFL/IVFL, IFL/IML; *A. montanus,* IFL/IML, IVML/IML; *A. pugnax,* IVTL/IVTarL, IVML/IVTarL. The very sparse setation of the pars thoracica, the small setaless area on the upper ectal surface of the chelicerae, and the darker pigmentation on the abdominal dorsum distinguish this species from *A. hageni;* the latter two characters help separate *A. cerberus* from *A. montanus.*

Variation. Within the small species sample, there is no marked variation in any characters studied. *Females.* Noteworthy variation occurs in the slenderness of the seminal receptacle stalks and in the ratio, stalk length/bowl length. Most of the range of this variation is illustrated by Figures 301 and 302.

Distribution. Known only from the type locality in northeastern Washington (Map 2).

Records. WASHINGTON. *Stevens Co.:* Cedar Lake, N of Leadpoint, May 1962, 4♂, 5♀. Another collection of 3 males made during "April to June" 1968 by H. Cusic at the same locality has been reported to me (W. Ivie, personal communication), but not examined.

Antrodiaetus yesoensis (Uyemura)

Figures 142, 165, 183, 222–223, 260–261, 303. Map 3.

Acattyma yesoensis Uyemura, 1942 Acta Arach., 7(1): 31, pls. 1–2. Holotype male from Yafugyu Tyo, Kitamiguni, Hokkaido, Japan, 15 June 1941; destroyed during World War II (Yaginuma, 1957). –Yaginuma, 1957, Acta Arach., 14(2): 52, pl. 3, fig. 1.

Antrodiaetus yesoensis: Yaginuma, 1960, Spiders of Japan in Colour, p. 20, fig. 13, pl. 1, fig. 3.

Description. See Tables 12–14, which contain measurements, meristic data, and diagnostic ratios for a sample of the species. Unfortunately this description is based on two males and only one female. The female specimen is possibly immature, but is nevertheless included since no females of this species have heretofore been described.

Male. Carapace: Setae sparse on pars thoracica. *Chelicerae:* Large setaless area on upper ectal surface. *Pedipalps:* Figures 183, 222, 223. Tibia strongly swollen in lateral view; greatest diameter in lateral view near midpoint. Tip of o.c.s. of palpus blunt and closely appressed to i.c.s. Tip of i.c.s. well sclerotized and weakly curved. *Leg I:* Figures 260, 261. Large dense group of macrosetae (great majority ensiform) centered at 1/2 to 2/3 of distance from proximal to distal end of tibia on prolateral surface. Small group of scattered macrosetae on retrolateral aspect of ventral surface of distal half of tibia. Macrosetae absent on ventral surface between these two groups. Tibia bowed laterally so that prolateral surface convex. No macrosetae on metatarsus. Metatarsus relatively short; in ventral view tapered toward distal end and sinuous. *Abdomen:* 3 broadly continuous, dorsal, heavily sclerotized patches. *Coloration:* Carapace light brown; border between pars cephalica and pars thoracica slightly darker. Sternum and pedipalpal coxae pale yellow-gray; labium a darker light brown. Chelicerae slightly lighter than carapace. Patella, tibia, and metatarsus of leg I very dark red-brown; femur lighter red-brown, but darker than carapace. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Posterior-dorsal surface of abdomen and dorsal sclerotized patches medium brown or gray-brown; rest light gray-yellow.

Female. Carapace: Setae sparse on pars thoracica, densest along lateral border. *Sternum:* Figure 142. *Chelicerae:* Figure 165. Microteeth relatively small; positioned beside last 5 macroteeth. Large setaless area on upper ectal surface. *Genitalia:* Figure 303. Seminal receptacles with only moderately sclerotized and somewhat elongate stalk and bowl; bowl weakly developed. Border of bowl with bulb not sharply defined. Bursa copulatrix very weakly sclerotized. *Coloration:* Carapace gray-yellow to light brown; pars thoracica slightly lighter than pars cephalica. Sternum similar to pars thoracica. Labium, pedipalpal coxae, and chelicerae almost medium brown, darker than carapace. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray; tergite darker, similar to pars thoracica.

Diagnosis. Males. The shapes and the macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 260, 261; Table 12) are in combination distinctive for this species. Because of the relatively short metatarsus and tarsus of leg I (Fig. 261), the ratios and measurements ITL/IML, IML, IML/ITarL, ITL/ITarL and ITarL (Table 13) are very helpful in separating this species from others in the *unicolor* group. The strongly swollen pedipalpal tibia and the relatively short pedipalpal femur (Fig. 183) are features also useful in identifying this species (PTT/PTL, PTL, and PFL/CL; Table 13). *Females.* On the basis of the single, possibly immature specimen available, the following character states best separate this species from others in the *unicolor* group: 1) Low CMT and IVMT numbers (Fig. 165, Table 14). 2) Some proportionately short leg segments resulting in some potentially useful leg segment ratios (Table 14). 3) Relatively long seminal receptacles with poorly developed bowls (Fig. 303). With a larger, definitely adult sample, it is likely that few of these characters will prove to be diagnostic.

Distribution. The Japanese island of Hokkaido (Map 3).

Records. JAPAN. *Hokkaido:* Abashiri, 12 Aug. 1955, ♂. — Asahigawa, 26 Aug. 1961, ♂. — ♀. In addition to the holotype male record (Yafugyu Tyo, Kitamiguni, Hokkaido, 15 June 1941), a few other *A. yesoensis* records, all from Hokkaido, are listed in the literature (Yaginuma, 1957 and 1960).

THE *LINCOLNIANUS* GROUP

Descriptive diagnosis. Male: AMD proportionately small to medium; AME's well separated (AMD/AMS, AMD/CL; Table 13). Setae scattered over much of labium; setaless area just posterior of labium relatively small. Pedipalpal tibia elongate (PTT/PTL, Table 13); greatest diameter in lateral view distal of midpoint. O.c.s. of palpus weakly to moderately heavily sclerotized; surface smooth to weakly file-like; relatively narrow apically. Relatively inconspicuous group of enlarged setae on prolateral surface of tibia I. *Female:* Carapace moderately to quite broad (CW/CL, Table 14). Labium setation as in male. Cheliceral microteeth proportionately large and numerous (CMT, Table 14). Tarsus IV claws (both prolateral and retrolateral) usually with only 0 to 2 teeth (IVCTR, Table 14). Leg IV segments proportionately short, particularly femur and metatarsus (IVML/CL, Table

14). Bursa copulatrix lacks median partition; lining very weakly sclerotized. Seminal receptacles small in proportion to body size, stalk short to moderately long, bowl poorly to well developed, and receptacles not closely paired.

Antrodiaetus lincolnianus (Worley)

Figures 119, 127, 135, 152, 166, 184, 224–225, 262–263, 304–305. Map 1.

Brachybothrium lincolnianum Worley, 1928, Ann. Ent. Soc. America, 21(4): 619, fig. 1. Holotype male and 3 male paratypes from Lincoln, Lancaster Co., Nebraska, March and April 1923. Holotype and 2 of 3 paratypes are in the Museum of Comparative Zoology; examined. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Figure 127. Broad. *Chelicerae:* Figure 152. *Pedipalps:* Figures 184, 224, 225. Femur, patella, particularly tibia markedly elongate. Greatest diameter of tibia in lateral view at approximately 2/3 of distance from proximal to distal end. O.c.s. of palpus weakly sclerotized; surface nearly smooth; tip very thin, spatulate and erect. Tip of i.c.s. weakly sclerotized, short and straight; even with tip of o.c.s. in unflexed condition. Sperm reservoir looped very loosely. (Left palpus of holotype missing and tips of both o.c.s. and i.c.s. of right palpus are partially broken.) *Leg I:* Figures 262, 263. Distal 1/2 to 1/3 of prolateral surface of tibia with group of enlarged, decumbent, attenuate setae. Tibia slightly swollen near distal end. Metatarsus with 2 (rarely 1) usually attenuate macrosetae ventrally at distal end. Metatarsus nearly straight; slightly shortened and thickened. *Abdomen:* 3 continuous, dorsal, heavily sclerotized patches; second patch largest. *Coloration:* Carapace medium brown to darker red-brown. Sternum, labium, and pedipalpal coxae pale yellow-gray. Chelicerae medium brown. Pedipalps and legs dorsally similar to carapace, ventrally lighter; leg I darkest. Abdomen medium brown to dark gray; tergite lighter gray-yellow.

Female. Carapace: Figures 119, 135. Broad. *Chelicerae:* Figures 119, 166. Microteeth positioned beside last 6 macroteeth and sometimes extending beyond last macrotooth. *Genitalia:* Figures 304, 305. Seminal receptacles with very short, weakly sclerotized stalk and weakly developed bowl; border of bowl with bulb not sharply defined. *Coloration:* Pars cephalica light brown to medium brown; pars thoracica slightly paler. Sternum similar to pars thoracica; labium and pedipalpal coxae darker. Chelicerae medium to dark orange-brown or brown. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen medium brown; tergite yellow-gray. (The observed specimens have been in alcohol over 18 years and may be significantly discolored.)

Diagnosis. Males. The very elongate slender pedipalpal tibia (Fig. 184) (PTT/PTL, Table 13), the palpus structure (Figs. 224, 225), and the small AME (AMD/AMS, AMD, AMD/CL, etc., Table 13) are distinctive for this species. The group of enlarged setae on the prolateral surface of tibia I consists of setae that are more decumbent and usually shorter (Fig. 262) than those of *A. stygius* and *A. apachecus*. Also, the darker abdominal coloration and frequent possession of metatarsal macroseta B help distinguish this species from *A. stygius* and *A. apachecus*. *Females.* (It must be kept in mind that the female samples for the *lincolnianus* group species are quite small; a future analysis of larger samples may show that some or all of the few characters now listed as diagnostic are not diagnostic.) *A. lincolnianus* has a larger CMT number and smaller IVMT number than *A. stygius* or *A. apachecus*. The stalk and bowl portion of *A. lincolnianus* seminal receptacles is more weakly sclerotized and smaller, and its border with the bulb less well defined (Figs. 304, 305) than that of the other *lincolnianus* group species. Also the carapace of *A. lincolnianus* (Fig. 119) is broader than that of *A. stygius* (CW/CL, Table 14).

Variation. Variation in both sexes within the available species sample is small for all characters studied.

Distribution. Eastern Kansas and eastern Nebraska (Map 1).

Records. KANSAS. *Jefferson Co.:* Kansas Univ. Nat. Hist. Reservation near Lawrence. 28 Feb. 1964, ♂. NEBRASKA. *Lancaster Co.:* Lincoln, 5–19 April 1923, 3♂; 18 Mar. 1926, ♂; 18 Mar. 1951, ♂; 2♀. Two unexamined literature records (Scheffer, 1906), almost certainly of misidentified *A. lincolnianus* specimens (Scheffer misidentified the specimens as *Brachybothrium robustum* Simon.), are worth adding tentatively. KANSAS. *Ottawa Co.:* Delphos. *Riley Co.:* Manhattan, 5 April, 2♂.

Antrodiaetus stygius new species

Figures 117–118, 128, 136, 143, 153, 167, 185, 226–228, 264–265, 306–307.
Map 1.

Antrodiaetus lincolnianus: Peck (not Worley, 1928), 1966, American Midl. Nat., 76(1): 153.

Type specimens. Holotype male from Bennett Springs State Park, Dallas Co., Missouri, 4 September 1967 (F. A. Coyle), in the Museum of Comparative Zoology. Four males and 3 females from type locality with same date designated as paratypes and deposited in MCZ and AMNH. The specific name is a Latin adjective meaning "Stygian."

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Figure 128. Somewhat narrowed. *Chelicerae:* Figure 153. Anterior-dorsal prominence weak. *Pedipalps:* Figures 185, 226–228. Tibia somewhat elongate; greatest diameter in lateral view at between 1/2 to 2/3 of distance from proximal to distal end. O.c.s. of palpus moderately strongly sclerotized; surface roughened distally but not filelike; tip thin, spatulate, and bent away from i.c.s. Tip of i.c.s. relatively well sclerotized, gradually tapering, and rather strongly curved; extends well beyond tip of o.c.s. in unflexed condition. Sperm reservoir looped tightly. *Leg I:* Figures 264, 265. Distal 2/3 of prolateral surface of tibia with group of scattered, enlarged, erect attenuate setae. Tibia not swollen distally. Metatarsus with or without 1 attenuate macroseta ventrally at distal end. Metatarsus rather slender and slightly sinuous in ventral view. *Abdomen:* 3 sometimes continuous, dorsal, heavily sclerotized patches; third patch smallest, sometimes faint or consisting of bilateral pair of small patches. *Coloration:* Pars cephalica light brown to medium brown; pars thoracica paler yellow-gray. Sternum and palpal coxae slightly lighter than pars thoracica. Labium and chelicerae slightly lighter than pars cephalica. Pedipalps and legs dorsally similar to adjacent part of carapace, ventrally like sternum. Abdominal dorsum pale yellow-gray; tergite darker yellow-gray.

Female. Carapace: Figures 117, 118, 136. Somewhat narrowed. *Sternum:* Figure 143. *Chelicerae:* Figures 117, 118, 167. Microteeth positioned beside last 7 to last 6 macroteeth, except sometimes not extending beyond penultimate macrotooth. *Genitalia:* Figures 306, 307. Seminal receptacles with well-sclerotized stalk and bowl; border of bowl with bulb well defined. *Coloration:* Pars cephalica medium brown; pars thoracica paler yellow-gray. Sternum similar to pars cephalica; labium and palpal coxae darker brown. Chelicerae dark brown. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray; tergite darker yellow-gray.

Diagnosis. Males. The palpus structure (particularly the form of the o.c.s. tip) (Figs. 226–228) distinguishes this species from both *A. lincolnianus* and *A. apachecus.* Because of its relatively long tarsus I and metatarsus I (Fig. 265), this species can be readily separated from *A. lincolnianus* by ITL/IML and ITL/ITarL (Table 13); IFL/ITarL and ITL/ITarL (Table 13) help to separate it from *A. apachecus.* CW/CL aids separation of *A. stygius* from the broader carapaced *A. lincolnianus. Females.* IVML/CL and IML/CL (Table 14) help separate this species, with its proportionately short metatarsi, from *A. lincolnianus.*

Variation. Males. There is substantial variation in the shape and prominence of the anterior-dorsal protuberance of the chelicerae, but such variation is continuous and as extensive within the type locality sample as within the whole species sample. The chelicerae of most specimens are similar to Figure 153. The palpi of the Warrensburg, Missouri, and Imboden, Arkansas, specimens are less heavily sclerotized than those in the type locality sample. Most of the variation in the form of the o.c.s. tip falls within the range illustrated by Figures 227 and 228. *Females.* Figures 306 and 307 illustrate the range of seminal receptacle form in the three brooding females.

Distribution. Missouri and northern Arkansas (Map 1).

Records. ARKANSAS. *Lawrence Co.:* Imboden, 1935, 2♂. MISSOURI. *Dallas Co.:* Bennett Springs St. Pk., 4 Sept. 1967, 5(♂), 3♀. *Johnson Co:* Warrensburg, 1–10 Oct. 1962, ♂.

Antrodiaetus apachecus new species

Figures 154–156, 168, 186, 229–232, 266–267, 308–309. Map 4.

Type specimens. Holotype male from Wet Canyon (about 4 mi. SE of Mount Graham), Graham Mountains, Graham Co., Arizona, 14 September 1950 (W. J. Gertsch), in the American Museum of Natural History. Two males and 1 female from type locality with same date designated as paratypes and deposited in MCZ and AMNH. The specific name is derived from the name of the Apache Indian tribe.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Chelicerae: Figures 154–156. *Pedipalps:* Figures 186, 229–232. Tibia somewhat elongate; greatest diameter in lateral view at between 5/8 to 2/3 of distance from proximal to distal end. O.c.s. of palpus moderately strongly sclerotized; surface roughened distally, sometimes weakly filelike; tip moderately thickened and erect. Tip of i.c.s. relatively well sclerotized, gradually tapering, and curved; extends far beyond tip of o.c.s. in unflexed condition. Sperm reservoir looped tightly. *Leg I:* Figures 266, 267. Distal 2/3 of prolateral surface of tibia with group of scattered, enlarged, suberect attenuate setae. Tibia not swollen distally. Metatarsus with 1 (rarely without) attenuate or ensiform macroseta positioned ventrally at distal end. Metatarsus very slightly sinuous in ventral view. *Abdomen:* 3 frequently continuous, dorsal, heavily sclerotized patches; third patch smallest and most weakly sclerotized, sometimes consisting of bilateral pair of small patches. *Coloration:* Pars cephalica light brown to medium brown; pars thoracica slightly lighter. Sternum pale gray-yellow; labium and palpal coxae slightly darker gray-yellow. Chelicerae similar to pars thoracica. Pedipalps and legs dorsally similar to carapace, ventrally lighter; leg I darkest. Abdomen gray-yellow or yellow-gray; tergites darker yellow-gray or brown.

Female. Chelicerae: Figure 168. Microteeth positioned beside last 8 to last 5 macroteeth and sometimes extend beyond last macrotooth. *Genitalia:* Figures 308, 309. Seminal receptacles with well-sclerotized stalk and bowl; border of bowl with bulb rather well defined. *Coloration:* Carapace yellow-gray to light brown; pars cephalica often slightly darker than pars thoracica. Sternum similar to pars thoracica; labium and palpal coxae darker. Chelicerae light brown to medium brown. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen yellow-gray; tergite darker yellow-gray.

Diagnosis. Males. The palpus structure (particularly the form of the o.e.s. tip) (Figs. 229–232) distinguishes this species from both *A. lincolnianus* and *A. stygius.* The enlarged setae on the prolateral surface of tibia I are less erect in this species (Fig. 266) than in *A. stygius.* The normally large EGS number of this species (Table 13) may also help separate it from *A. stygius. Females.* The following ratios help distinguish this species, with its relatively long leg I and short leg IV segments, from the other *lincolnianus* group species (Table 14): IFL/IVFL and IVML/IML (from *A. stygius*); IVML/CL and IVTL/CL (from *A. lincolnianus*).

Variation. Males. Substantial variation occurs in the anterior-dorsal profile of the chelicerae, with most of the specimens similar to those in Figure 156. Much of the total range of this variation occurs within the Alpine, Arizona, sample (Figs. 154, 155). The slenderness of the pedipalpal tibia varies considerably. The PTT/PTL range for the three Graham Mountain, Arizona, specimens is 0.324–0.343. PTT/PTL values of three other specimens fall within this range. However, the other two known specimens (from near La Cueva, New Mexico, and Heber, Arizona) have PTT/PTL values of 0.308 and 0.297 respectively. Figures 230–232 illustrate most of the variation observed in the shape of the o.e.s. tip. There is noteworthy variation in the maximum size of the enlarged setae on the prolateral surface of tibia I; on several specimens these setae are only slightly larger than the background setae. *Females.* The bowl portion of the seminal receptacles is not as well developed in the Flagstaff, Arizona, specimen (Fig. 308) as in the Graham Mountain, Arizona, specimen (Fig. 309). There is considerable variation in AME diameter (Table 14).

Since *A. apachecus* is apparently limited to forest habitats which presently occur only at high elevations in the southwestern U. S., it consists of at least several populations each separated by extensive areas of lower unfavorable dry habitats. Consequently the gene flow between these populations is probably greatly reduced, certainly part of the explanation for the geographic variation indicated by the few specimens presently available.

Distribution. Mountains of Arizona and New Mexico (Map 4).

Records. ARIZONA. *Apache Co.:* ♀; 4 mi. N of Alpine, Alpine Divide Campgrd., 8500 ft, 18 July 1965, 2♂. *Cochise Co.:* Chiricahua Mtns., Rustlers Camp, 19 Aug. 1955, ♂. *Coconino Co.:* Flagstaff, ♀. *Graham Co.:* Graham Mtns., Wet Canyon, 14 Sept. 1950, 3♂, ♀. *Navajo Co.:* 6 mi. N of Heber, Overgaard Camp, 17 Sept. 1950, ♂. NEW MEXICO. *Sandoval Co.:* 2 mi. NW of La Cueva, Horseshoe Springs Campgrd., 7800 ft, 31 July 1961, ♂.

THE *RORETZI* GROUP

Antrodiaetus roretzi (L. Koch)

Figures 114–116, 129, 137, 144, 157, 169, 187, 233, 268–269, 310–312. Map 3.

Acattyma Roretzii L. Koch, 1878, Verh. zool.-bot. Ges. Wien, 27: 761, pl. 16, figs. 23–25. Two immature female syntypes from Japan; in the British Museum of Natural History; both examined. These are now designated lectotype and paralectotype and are so labeled. –Uyemura, 1942, Acta Arach., 7(1): 31, 35, 36, fig. p. 37.

Acattyma roretzii: Komatsu, 1942, Acta Arach., 7(2): 57. –Roewer, 1942, Katalog der Araneae, 1: 189. –Komatsu, 1961, Arach. Soc. E. Asia, p. 7, pl. 1, fig. 1.

Acattyma roretzi: Pocock, 1901, Proc. Zool. Soc. London, 1: 207, 211. –Bonnet, 1955, Bibliographia Araneorum, 2: 141.

Antrodiaetus roretzi: Yaginuma, 1960, Spiders of Japan in Colour, p. 19, fig. 14, pl. 1, fig. 2.

Description. See Tables 12–14, which contain measurements, meristic data, and diagnostic ratios for a sample of the species.

Male. Carapace: Figures 114, 129. Proportionately broad. Ocular tubercle projects strongly forward. Few setae on pars thoracica. *Sternum:* Similar to female sternum. *Chelicerae:* Figures 114, 157. Anterior-dorsal prominence broadly rounded. Upper ectal setation as in female. *Pedipalps:* Figures 187, 233. Tibia moderately swollen in lateral view; greatest diameter in lateral view just proximal of midpoint. O.c.s. of palpus heavily sclerotized, very broad, and curved in cross section to partially envelop i.c.s.; much of surface file-like, particularly at tip. I.c.s. extends slightly beyond tip of o.c.s. in unflexed condition; i.c.s. tip well sclerotized and straight. *Leg I:* Figures 268, 269. Group of long erect macrosetae (all attenuate) centered just proximal of midpoint of tibia on prolateral surface and prolateral aspect of ventral surface. Other macrosetae rare or absent on tibia. Tibia weakly bowed downward. No macrosetae on metatarsus. Metatarsus weakly sinuous in ventral view. *Abdomen:* 2 dorsal, heavily sclerotized, noncontinuous patches with transverse row of 2–4 tiny sclerotized spots behind second patch. Second patch much larger and thicker than first. *Coloration:* Carapace pale orange-brown to darker red-brown; pars cephalica darker than pars thoracica. Sternum and pedipalpal coxae like pars thoracica. Labium and chelicerae brown to dark red-brown; darker than pars cephalica. Patella and more distal segments of leg I similar to chelicerae; femur dorsally almost as dark, ventrally lighter. Pedipalps and other legs dorsally similar to adjacent part of carapace, ventrally lighter. Abdominal dorsum yellow-gray; tergite yellow-brown.

Female. Carapace: Figures 115, 116, 137. Proportionately broad. Few setae on pars thoracica. *Sternum:* Figure 144. Broad. Relatively large area just posterior to labium and all of labium (except anterior and lateral border) devoid of setae. *Chelicerae:* Figures 115, 116, 169. Microteeth positioned beside last 6 to last 4 macroteeth; occasionally extend beyond last macrotooth. Microteeth quite small. Large area on upper ectal surface devoid of setae. *Genitalia:* Figures 310–312. Seminal receptacles with rather weakly sclerotized stalk and bowl. Stalk long and relatively slender; not expanded at base. Bowl weakly developed; its border with bulb weakly defined. Receptacles clearly paired with each pair opening into widely separate parts of bursa copulatrix. Median partition divides bursa copulatrix into two lateral pockets. *Coloration:* Carapace and sternum orange-brown. Labium, pedipalpal coxae, and chelicerae darker brown. Pedipalps and legs dorsally similar to carapace, ventrally slightly lighter. Abdominal dorsum light gray-brown; tergite darker orange-brown.

Diagnosis. Males. The extremely wide palpal o.c.s. (Fig. 233) distinguishes this species from all other *Antrodiaetus* species. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I are also distinctive (Table 12); no other *Antrodiaetus* species has such long erect macrosetae in the prolateral tibia I macrosetae group or has this group centered proximal of the midpoint (Fig. 268). The absence of other tibia I macrosetae separates *A. roretzi* from the *unicolor* group species. The rather large setaless area on the labium and adjacent part of the sternum and, to a lesser extent, the form of the carapace (Fig. 114) are distinctive. Because of *A. roretzi's* proportionately long metatarsus I (Fig. 269), ratios such as IML/CL, ITL/IML, and IML/ITarL (Table 13) will separate this species from most other *Antrodiaetus* species.

Females. The division of the bursa copulatrix into two lateral pouches by a median partition (Fig. 312) distinguishes *A. roretzi* from all other *Antrodiaetus* species. The combination of a long slender seminal receptacle stalk, a weakly developed bowl, and the closely paired nature of the seminal receptacles (Figs. 310, 311) is also distinctive. (Only some eastern *A. pacificus* females approach this condition.) The setaless area on the labium and adjacent part of the sternum is proportionately larger than on all other *Antrodiaetus* species. Low CMT number (Fig. 169, Table 14) distinguishes this species from most others. CW/CL (Table 14) separates this species, with its broad carapace and sternum (Figs. 115, 144), from most *unicolor* group species. The cheliceral microteeth are markedly smaller (Fig. 169) than those of the *lincolnianus* group species and there are more (3–4) leg IV claw teeth.

Distribution. Central portion of the Japanese island of Honshu (Map 3).

Records. JAPAN (Honshu Island). *Kanagawa Pref.:* Yokohama, 2 Dec. 1942, ♂. *Mie Pref. Nagano Pref. Saitama Pref.:* 3 May, 1957, ♂. *Tochigi Pref.:* 2♀. There are literature records for this species from Tokyo Pref. and Gifu Pref. (S side of Mt. Kinkazan) as well as literature records of some of the prefectures listed above (Komatsu, 1942 and 1961; Ohe, 1966; Uyemura, 1936; Yaginuma, 1960 and 1962; Yamamoto, 1942).

Aliatypus Smith, 1908

Aliatypus Smith, 1908, Ann. Ent. Soc. America, 1(4): 231. Type species by monotypy *Atypoides californicus* Banks, 1896, Jour. New York Ent. Soc., 4(4): 88. –Bonnet, 1955, Bibliographia Araneorum, 2(1): 225.

Descriptive diagnosis. Carapace: Figures 319, 320. Thoracic groove either an irregular pit (may be transverse or weakly longitudinal), reduced to a shallow depression, or absent. Usually a large seta medially on ocular prominence just anterior to AME's. *Sternum:* Figure 321. Labium usually proportionately small and strongly inclined from plane of sternum. *Chelicerae:* Figures 322, 323. Female with row of 6 to 9 macroteeth on prolateral side of closed fang; another row of 3–6 macroteeth on retrolateral side. Microteeth scattered between these rows. Female rastellum very strong. Male without anterior-dorsal prominence. *Pedipalps:* Figures 324, 325. Male patella very elongate, nearly as long as tibia; tibia elongate and swollen. O.c.s. and i.c.s. of palpus relatively weakly to moderately sclerotized. One edge of o.c.s. folded for most of its length to enclose embolus. I.c.s. extends to but not beyond o.c.s. tip; intimately combined distally with o.c.s. to envelop embolus. *Legs:* Figures 326, 327. One to 4 (rarely more than 1) trichobothria dorsally on female metatarsus IV. Zero to 2 (usually 0) teeth on each of prolateral and retrolateral claws of female tarsus IV. Male tibia I and metatarsus I with macrosetae scattered ventrally over most of length of both segments. *Spinnerets:* Figure 328. Three pairs (AL, PM, PL); all functional; AL's 2-segmented (segmentation may be vestigial) with at least several spigots clustered at tip of distal segment. *Genitalia:* Figures 329, 330. Bursa copulatrix very weakly sclerotized and often bilobed anteriorly. Seminal receptacles paired; uniformly un- or very weakly sclerotized; stalks very narrow, sinuous. *Behavior:* Burrow entrance a trapdoor.

Remarks. This genus, which contains a single described species, *Aliatypus californicus* (see Smith, 1908; Gertsch, 1949), and several undescribed species, has not been found outside of southern California. Its populations appear to be widely scattered from the San Francisco Bay region and the central Sierra Nevada Mountains south to near the Mexican border. A revision of *Aliatypus* is in preparation.

TABLE 12. MACROSETATION OF TIBIA AND METARSUS OF MALE LEG I OF *ANTRODIAETUS* SPECIES. See Fig. 70 for identification of metatarsal macrosetae. The number of legs (out of the total given with a particular pattern) also with a macroseta E (= *) or F (= √) are given in parentheses. Range and median given for tibia macrosetae groups.

			Metatarsal macrosetae pattern frequency distribution								
	N	N legs	Absent	A	AB	ABC	ABCD	ABD	AC	ACD	AD
*unicolor**	110	195	15	145(1)	1				26(1)	6(3)	1(1)
robustus	14	28		5	20	2			1		
*pacificus**	106	106	103						3(3)		
occultus	21	21	21								
pugnax√	24	24		6	13(5)	2(2)	2(2)	1(1)			
montanus	26	26	4	21						1	
hageni	8	15	1	6	6			2			
cerberus	4	8		1	7						
yesoensis	2	4	4								
lincolnianus	6	12		1	11						
stygius	8	16	6	10							
apachecus	8	16	4	12							
roretzi	2	3	3								

			Tibia macrosetae groups					
			Number of macrosetae in prolateral group			Number of macrosetae in retrolat.-vent. group		
	N	N legs	Total	Ensiform	% ensi.	Total	Ensiform	% ensi.
unicolor	110	195	5–49 21	4–36 14	33–100	3–8 5	0–8 3	0–100
robustus	14	23	11–35 16	0–1 0	0–8	5–10 6	0–1 0	0–17
pacificus	106	106	15–55 38	0–7 0	0–27	3–17 9	0–8 1	0–100
occultus	21	21	19–38 29	7–23 14	37–74	2–9 5	0–3 1	0–60
pugnax	24	24	10–21 15	9–17 12	67–100	2–9 6	2–7 5	50–100
montanus	26	26	14–44 28	9–36 21	48–93	6–23 14	2–13 7	33–86
hageni	8	8	15–56 37	15–56 37	93–100	11–16 14	11–16 14	87–100
cerberus	4	8	15–26 17	15–26 17	88–100	6–14 8	6–12 8	86–100
yesoensis	2	4	36–50 46	35–45 41	88–95	7	3–7 5	43–100
lincolnianus	6	6	0			0		
stygius	8	8	0			0		
apachecus	8	8	0			0		
roretzi	2	3	20–25 24	0	0	0		

Table 13. Measurements, meristic character, and diagnostic ratios for adult males of *Antrodiaetus* species. The most useful diagnostic characters are circled. Range, mean, and standard deviation given for measurement characters (in mm) and ratios. Range and mean given for EGS. (EGS could be tallied on only one *A. lincolnianus* specimen.)

	N	CL	CW	OQW	ALS	ALD	AMS
unicolor	104	4.0-6.6 5.47±.57	2.97-5.24 4.241±.479	0.82-1.34 1.104±.102	0.38-0.63 0.498±.053	0.23-0.41 0.330±.036	0.07-0.19 0.132±.027
robustus	11	5.4-6.6 6.03±.38	4.33-5.27 4.800±.318	1.07-1.35 1.192±.093	0.47-0.66 0.564±.059	0.28-0.40 0.350±.037	0.11-0.22 0.153±.033
pacificus	105	4.1-6.9 5.61±.61	3.20-5.50 4.498±.486	0.83-1.32 1.082±.101	0.40-0.68 0.515±.057	0.26-0.47 0.343±.043	0.08-0.24 0.140±.038
occultus	21	4.2-6.2 5.32±.50	3.50-5.01 4.310±.389	0.95-1.23 1.092±.088	0.43-0.60 0.510±.042	0.27-0.37 0.333±.036	0.11-0.18 0.146±.020
pugnax	24	4.2-5.6 4.90±.43	3.31-4.56 3.875±.397	0.78-1.06 0.947±.083	0.39-0.57 0.457±.050	0.24-0.36 0.310±.030	0.11-0.20 0.140±.029
montanus	23	5.0-7.0 5.82±.51	4.07-5.80 4.847±.436	0.95-1.17 1.064±.057	0.49-0.63 0.565±.037	0.24-0.33 0.290±.031	0.11-0.22 0.177±.029
hageni	8	5.5-6.3 5.88±.30	4.29-5.24 4.772±.343	0.88-1.15 1.002±.093	0.40-0.57 0.497±.054	0.28-0.34 0.311±.022	0.14-0.18 0.160±.012
cerberus	4	5.2-5.4 5.26	4.18-4.44 4.265	0.90-0.95 0.930	0.45-0.47 0.457	0.25-0.31 0.275	0.15-0.18 0.162
yesoensis	2	4.6-5.1 4.85	3.73-4.07 3.900	1.06 1.060	0.42-0.51 0.465	0.27-0.33 0.300	0.16-0.17 0.165
lincolnianus	6	4.6-5.7 5.06±.40	3.92-4.86 4.263±.342	0.82-1.01 0.905±.065	0.40-0.53 0.455±.043	0.21-0.25 0.230±.013	0.18-0.22 0.205±.016
stygius	8	4.0-5.0 4.64±.36	3.24-4.07 3.606±.268	0.79-0.96 0.886±.058	0.40-0.47 0.435±.024	0.23-0.29 0.259±.019	0.18-0.22 0.192±.014
apachecus	8	4.6-5.4 5.00±.37	3.73-4.67 4.054±.322	0.83-1.07 0.931±.086	0.42-0.56 0.476±.053	0.24-0.30 0.266±.021	0.14-0.26 0.195±.043
roretzi	2	5.1-5.3 5.19	4.18-4.52 4.350	1.01-1.03 1.020	0.48-0.53 0.505	0.29-0.30 0.295	0.13-0.14 0.135

	AMD	IFL	ITL	IML	ITarL	PFL	PTL
unicolor	0.11-0.20 0.158±.017	3.84-6.40 5.097±.466	2.56-4.22 3.438±.394	3.01-5.35 4.280±.556	1.80-2.78 2.314±.219	2.33-3.92 3.215±.384	2.14-3.50 2.878±.368
robustus	0.14-0.18 0.162±.013	5.05-6.06 5.537±.321	3.31-3.95 3.625±.221	3.99-4.93 4.539±.312	2.33-2.78 2.547±.159	3.27-3.92 3.665±.222	2.94-3.43 3.216±.162
pacificus	0.11-0.18 0.136±.024	3.84-6.25 5.109±.586	2.48-4.22 3.248±.407	3.16-5.80 4.540±.568	1.69-3.05 2.356±.300	2.78-4.52 3.709±.407	2.41-3.92 3.164±.333
occultus	0.13-0.19 0.158±.018	3.99-5.73 4.801±.436	2.63-3.69 3.133±.278	3.09-4.22 3.671±.331	1.88-2.41 2.153±.178	2.78-3.88 3.297±.265	2.45-3.39 2.882±.250
pugnax	0.11-0.14 0.120±.008	3.77-5.31 4.584±.421	2.56-3.54 3.113±.281	2.86-4.07 3.561±.347	1.69-2.75 2.235±.247	2.60-3.77 3.065±.331	2.33-3.20 2.798±.240
montanus	0.11-0.16 0.133±.012	5.31-6.82 5.998±.464	3.65-4.75 4.140±.315	4.18-5.57 4.732±.396	2.56-3.46 2.912±.228	3.54-4.67 3.999±.294	3.05-4.03 3.452±.262
hageni	0.11-0.12 0.119±.004	5.20-5.65 5.484±.179	3.58-3.95 3.779±.156	3.92-4.44 4.221±.172	2.37-2.78 2.616±.159	3.61-4.07 3.837±.139	3.27-3.54 3.377±.107
cerberus	0.09 0.090	4.82-5.27 5.010	3.24-3.61 3.360	3.46-3.92 3.605	1.96-2.18 2.032	3.09-3.24 3.135	2.56-2.75 2.607
yesoensis	0.11 0.110	4.26-4.56 4.410	3.01-3.20 3.105	3.16-3.24 3.200	1.92-1.96 1.940	2.71-3.01 2.860	2.48-2.56 2.520
lincolnianus	0.05-0.07 0.063±.008	4.37-5.69 4.948±.431	3.09-4.07 3.522±.327	3.09-4.07 3.465±.334	1.80-2.07 1.925±.089	3.77-4.75 4.234±.165	3.39-4.26 3.774±.123
stygius	0.09-0.12 0.102±.010	4.10-5.31 4.660±.391	2.78-3.58 3.157±.246	2.97-3.95 3.520±.303	1.80-2.41 2.107±.202	3.31-3.95 3.585±.215	2.86-3.31 3.050±.163
apachecus	0.09-0.11 0.102±.009	4.41-5.84 4.915±.478	3.09-3.92 3.342±.285	3.16-4.33 3.561±.446	1.80-2.48 2.039±.239	3.43-4.44 3.680±.331	2.82-3.61 3.025±.250
roretzi	0.13-0.14 0.135	5.08-5.12 5.100	3.20-3.27 3.235	4.22-4.37 4.295	2.11 2.110	3.61 3.610	2.78 2.780

Table 13 (continued).

	PTT	EGS	AMD/CL	AMD/AMS	ITL/CL	IML/CL	IFL/IML
unicolor	0.98-1.58 1.291±.112	12-51 25.7	0.022-0.035 0.029± .003	0.67-2.42 1.251±.309	0.54-0.69 0.628±.028	0.67-0.88 0.780±.043	1.14-1.30 1.193±.041
robustus	1.25-1.52 1.388±.081	40-64 52.9	0.024-0.032 0.027± .002	0.73-1.54 1.100±.228	0.57-0.65 0.601±.022	0.72-0.83 0.753±.035	1.16-1.26 1.221±.031
pacificus	1.01-1.56 1.273±.112	17-56 33.8	0.018-0.030 0.024± .004	0.50-2.00 1.016±.316	0.51-0.70 0.578±.035	0.73-0.91 0.808±.042	1.03-1.22 1.128±.044
occultus	1.16-1.51 1.349±.103	10-40 22.5	0.026-0.033 0.030± .002	0.81-1.50 1.095±.162	0.57-0.62 0.589±.018	0.64-0.76 0.691±.027	1.25-1.38 1.308±.037
pugnax	1.03-1.32 1.165±.085	17-44 31.1	0.021-0.029 0.025± .002	0.60-1.18 0.883±.156	0.57-0.68 0.635±.027	0.64-0.81 0.727±.048	1.16-1.42 1.290±.083
montanus	1.20-1.45 1.308±.083	31-62 45.5	0.020-0.026 0.023± .002	0.59-1.09 0.770±.120	0.67-0.77 0.712±.019	0.77-0.87 0.814±.024	1.19-1.34 1.268±.036
hageni	1.23-1.41 1.326±.063	29-59 42.0	0.019-0.022 0.020± .001	0.67-0.80 0.745±.042	0.64-0.66 0.642±.013	0.70-0.74 0.718±.021	1.26-1.32 1.300±.020
cerberus	1.01-1.09 1.040	32-46 41.0	0.016-0.017 0.017	0.50-0.60 0.556	0.61-0.69 0.638	0.65-0.72 0.683	1.34-1.42 1.391
yesoensis	1.12-1.20 1.160	30-39 34.5	0.023 0.023	0.65-0.69 0.667	0.62-0.66 0.640	0.63-0.69 0.661	1.35-1.41 1.378
lincolnianus	0.81-1.01 0.897±.038	63	0.010-0.015 0.013± .002	0.27-0.37 0.309±.038	0.67-0.71 0.695±.018	0.67-0.71 0.683±.020	1.38-1.48 1.429±.036
stygius	0.90-1.05 0.982±.058	25-55 35.5	0.019-0.025 0.022± .002	0.45-0.63 0.533±.052	0.64-0.72 0.680±.027	0.71-0.79 0.758±.028	1.29-1.38 1.325±.029
apachecus	0.94-1.07 0.980±.048	32-69 50.8	0.016-0.024 0.021± .003	0.36-0.78 0.553±.149	0.63-0.72 0.668±.030	0.66-0.80 0.710±.042	1.27-1.49 1.385±.071
roretzi	1.09 1.090	22-39 30.5	0.024-0.026 0.026	1.00 1.000	0.62-0.63 0.623	0.82-0.83 0.827	1.17-1.20 1.188

	IFL/ITarL	ITL/IML	ITL/ITarL	IML/ITarL	PFL/CL	PTT/CL	PTT/PTL
unicolor	1.96-2.43 2.200±.114	0.74-0.85 0.805±.027	1.35-1.62 1.484±.068	1.60-2.06 1.845±.111	0.53-0.63 0.586±.022	0.20-0.27 0.237±.014	0.38-0.54 0.452±.038
robustus	2.11-2.33 2.176±.088	0.77-0.83 0.799±.019	1.36-1.53 1.424±.052	1.71-1.87 1.782±.050	0.58-0.65 0.608±.022	0.21-0.24 0.230±.008	0.40-0.47 0.432±.021
pacificus	1.84-2.46 2.174±.119	0.65-0.81 0.717±.041	1.26-1.53 1.381±.069	1.74-2.12 1.929±.106	0.61-0.71 0.661±.022	0.20-0.25 0.227±.014	0.33-0.48 0.404±.026
occultus	2.07-2.42 2.231±.115	0.81-0.90 0.854±.024	1.38-1.55 1.456±.063	1.60-1.84 1.706±.059	0.59-0.65 0.620±.019	0.23-0.27 0.254±.010	0.45-0.49 0.468±.016
pugnax	1.86-2.24 2.059±.116	0.82-0.91 0.875±.029	1.31-1.60 1.397±.053	1.48-1.74 1.597±.064	0.57-0.72 0.625±.036	0.22-0.25 0.238±.008	0.37-0.44 0.417±.013
montanus	1.98-2.20 2.061±.061	0.83-0.91 0.875±.018	1.36-1.50 1.422±.032	1.56-1.76 1.625±.046	0.63-0.73 0.688±.020	0.20-0.25 0.226±.013	0.35-0.40 0.380±.014
hageni	2.02-2.20 2.100±.071	0.88-0.90 0.895±.013	1.39-1.51 1.446±.043	1.56-1.70 1.616±.045	0.63-0.68 0.653±.021	0.21-0.23 0.225±.007	0.37-0.41 0.393±.011
cerberus	2.42-2.50 2.466	0.92-0.93 0.932	1.65-1.66 1.653	1.76-1.80 1.773	0.58-0.60 0.595	0.19-0.20 0.197	0.39-0.41 0.399
yesoensis	2.22-2.32 2.273	0.95-0.99 0.970	1.57-1.63 1.600	1.64-1.65 1.649	0.58-0.59 0.589	0.23-0.24 0.239	0.45-0.47 0.460
lincolnianus	2.43-2.75 2.567±.107	1.00-1.04 1.017±.018	1.71-1.96 1.826±.087	1.71-1.96 1.797±.094	0.81-0.87 0.837±.021	0.17-0.18 0.178±.005	0.23-0.24 0.238±.003
stygius	2.12-2.28 2.214±.061	0.87-0.94 0.898±.022	1.42-1.54 1.501±.042	1.60-1.75 1.672±.052	0.71-0.85 0.774±.041	0.20-0.22 0.212±.007	0.31-0.34 0.322±.011
apachecus	2.29-2.54 2.416±.074	0.89-0.99 0.943±.044	1.52-1.72 1.646±.007	1.64-1.86 1.746±.066	0.66-0.82 0.737±.053	0.18-0.21 0.196±.011	0.29-0.34 0.325±.015
roretzi	2.39-2.43 2.417	0.75-0.76 0.753	1.51-1.55 1.533	2.00-2.07 2.036	0.68-0.71 0.695	0.20-0.22 0.210	0.39 0.392

Table 14. Measurements, meristic characters, and diagnostic ratios for adult females of *Antrodiaetus* species. The most useful diagnostic characters are circled. Range, mean, and standard deviation given for measurement characters (in mm) and ratios. Range, mean, and mode given for meristic characters. Number of females containing large maturing eggs or with brood is given in parentheses after N. For the last 7 species the CT and CMT statistics include counts of both right and left chelicerae.

	N	CL	CW	OQW	ALS	ALD	AMS	AMD
unicolor	225(158)	5.4-10.7 7.38±.95	3.88-8.06 5.434±.758	1.08-2.02 1.447±.181	0.45-0.93 0.666±.083	0.27-0.57 0.381±.054	0.11-0.34 0.198±.036	0.11-0.22 0.159±.020
robustus	13(5)	6.2-9.3 7.26±.99	4.71-7.23 5.577±.810	1.33-1.83 1.506±.180	0.63-0.95 0.780±.097	0.29-0.45 0.374±.063	0.18-0.31 0.228±.035	0.14-0.20 0.160±.020
pacificus	56(24)	5.4-8.1 6.74±.59	4.07-6.37 5.160±.464	1.06-1.69 1.321±.114	0.47-0.77 0.621±.071	0.26-0.47 0.355±.043	0.12-0.29 0.184±.034	0.11-0.18 0.131±.018
pugnax	24(13)	4.2-5.9 5.02±.51	3.20-4.71 3.848±.413	0.87-1.29 1.057±.121	0.38-0.61 0.494±.070	0.23-0.36 0.309±.031	0.11-0.21 0.146±.029	0.09-0.14 0.112±.012
montanus	12(5)	6.9-9.2 8.14±.65	5.50-7.87 6.589±.703	1.34-1.83 1.532±.137	0.67-1.02 0.827±.091	0.33-0.45 0.387±.042	0.19-0.40 0.295±.055	0.12-0.18 0.157±.017
hageni	7(2)	6.5-8.3 7.54±.63	5.01-6.59 5.783±.586	1.20-1.58 1.386±.126	0.54-0.73 0.659±.065	0.34-0.47 0.396±.041	0.19-0.25 0.214±.026	0.12-0.16 0.140±.017
cerberus	4(2)	6.6-7.5 6.99	5.16-5.84 5.472	1.39-1.41 1.400	0.64-0.71 0.677	0.33-0.36 0.340	0.19-0.22 0.202	0.11-0.12 0.117
yesoensis	1(0)	5.5	4.41	1.12	0.57	0.31	0.20	0.11
lincolnianus	2(1)	6.7-6.9 6.84	5.35-5.73 5.540	1.32-1.34 1.330	0.61-0.66 0.635	0.29-0.33 0.310	0.24-0.25 0.245	0.09-0.11 0.100
stygius	3(3)	5.9-6.9 6.34	4.59-5.20 4.847	1.23-1.45 1.303	0.56-0.68 0.630	0.24-0.38 0.320	0.19-0.25 0.220	0.11-0.12 0.117
apachecus	3(0)	5.9-6.8 6.37	4.86-5.27 5.097	1.20-1.41 1.287	0.45-0.68 0.590	0.32-0.37 0.343	0.14-0.25 0.210	0.11-0.12 0.117
roretzi	2(0)	6.6-6.9 6.77	5.50-5.80 5.650	1.29-1.30 1.295	0.72-0.77 0.745	0.31-0.32 0.315	0.21 0.210	0.14-0.15 0.145

	SL	SW	IFL	ITL	IML	ITarL	IVFL	IVTL
unicolor	2.94-6.03 4.084±.587	2.45-5.08 3.444±.501	3.84-7.69 5.238±.672	2.29-4.71 3.191±.414	2.11-5.08 3.236±.423	1.13-2.26 1.629±.193	3.61-7.65 5.085±.643	2.10-4.37 2.970±.362
robustus	3.27-5.08 3.980±.582	3.01-4.44 3.532±.481	4.29-6.37 5.065±.664	2.52-3.84 2.969±.427	2.45-3.77 2.934±.433	1.28-1.88 1.512±.179	4.18-6.14 4.875±.629	2.33-3.50 2.763±.361
pacificus	3.01-4.90 3.903±.395	2.60-3.99 3.165±.298	4.07-6.22 5.094±.469	2.41-3.69 3.104±.301	2.48-3.88 3.150±.304	1.28-1.96 1.604±.160	3.69-5.76 4.609±.392	2.07-3.16 2.612±.216
pugnax	2.37-3.54 2.878±.312	2.07-2.97 2.461±.261	2.97-4.37 3.625±.406	1.77-2.63 2.199±.254	1.73-2.56 2.144±.262	0.90-1.28 1.084±.116	2.86-4.22 3.470±.366	1.62-2.48 2.030±.199
montanus	3.84-5.57 4.727±.470	3.39-5.05 4.190±.487	5.20-7.31 6.143±.636	3.16-4.52 3.804±.401	3.24-4.71 3.938±.443	1.54-2.07 1.759±.154	5.12-7.01 5.933±.564	3.05-4.07 3.486±.301
hageni	3.92-5.05 4.479±.393	3.20-3.84 3.551±.215	4.82-6.22 5.614±.447	2.97-3.84 3.439±.308	3.05-3.92 3.461±.290	1.47-1.84 1.677±.125	4.75-6.18 5.537±.474	2.82-3.61 3.229±.293
cerberus	3.92-4.29 4.085	3.24-3.61 3.425	5.12-5.73 5.367	3.01-3.39 3.190	2.94-3.27 3.105	1.50-1.65 1.577	4.86-5.35 5.077	2.90-3.16 3.012
yesoensis	3.24	2.71	3.99	2.37	2.33	1.13	3.88	2.18
lincolnianus	3.84-4.07 3.955	3.20-3.54 3.370	4.82-5.05 4.935	2.86-3.09 2.975	2.78-2.90 2.840	1.31-1.35 1.330	4.63-4.67 4.650	2.63-2.71 2.670
stygius	3.39-3.84 3.563	3.09-3.46 3.213	4.07-4.71 4.307	2.45-2.86 2.597	2.22-2.63 2.370	1.09-1.28 1.153	3.88-4.52 4.117	2.18-2.48 2.307
apachecus	3.61-4.10 3.813	3.24-3.39 3.300	4.22-4.97 4.683	2.60-3.05 2.873	2.45-2.86 2.687	1.28-1.47 1.343	3.88-4.41 4.193	2.26-2.41 2.360
roretzi	3.84-4.07 3.955	3.46-3.61 3.535	5.08-5.42 5.250	2.94-3.16 3.050	2.97-3.16 3.065	1.43-1.54 1.485	4.82-5.08 4.950	2.48-2.71 2.595

Table 14 (continued).

	IVML	IVTarL	CT	CMT	IVCTR	PTSP	PTSR	IMS	IVMT
unicolor	3.00-6.33 4.385±.527	1.28-2.03 1.664±.163	8-15 11.4(11)	6-23 12.0(12)	1-6 3.5(3)	5-10 6.9(7)	2-7 3.8(4)	9-15 11.6(11)	9-20 14.2(15)
robustus	3.35-4.86 3.942±.470	1.31-1.73 1.505±.125	11-14 12.1(11)	11-18 13.9(13)	2-5 3.6(3)	4-7 5.9(6)	3-4 3.5(3)	9-14 10.6(10)	10-17 12.9(13)
pacificus	3.05-4.82 3.918±.348	1.28-1.80 1.531±.114	9-14 10.9(11)	9-24 16.8(19)	1-6 4.0(4)	5-12 8.2(8)	3-5 3.9(4)	9-15 12.3(13)	9-21 15.1(14)
pugnax	2.56-3.69 3.018±.290	1.01-1.43 1.220±.109	9-14 11.3(11)	8-17 12.1(12)	4-6 4.2(4)	4-8 5.9(5)	2-5 3.2(3)	9-13 11.1(11)	8-15 12.2(12)
montanus	4.52-5.99 5.201±.456	1.65-2.11 1.789±.135	10-17 12.4(12)	16-29 21.9(23)	3-5 3.9(4)	6-9 7.5(7)	2-4 3.4(4)	12-16 12.9(13)	14-19 16.5(17)
hageni	3.99-5.24 4.810±.376	1.47-1.84 1.710±.139	11-12 12.0(12)	13-18 15.1(15)	2-5 4.0(4)	5-11 7.4(6)	3-7 4.3(3)	13-15 13.7(13)	11-17 15.0(15)
cerberus	4.26-4.71 4.510	1.47-1.58 1.512	11-13 12.0	12-19 15.7	4-5 4.5	6-8 6.7	3 3.0	11-13 11.7	12-18 15.0
yesoensis	3.16	1.24	11	7	4	8	4	10	9
lincolnianus	3.84-3.92 3.880	1.47-1.50 1.485	12-13 12.5	23-27 25.0	0-1 0.5	4-8 6.0	3-4 3.5	13 13.0	5-7 6.0
stygius	3.05-3.65 3.263	1.20-1.35 1.250	12-14 13.0	14-19 17.0	0-2 1.3	4-7 5.3	2-4 3.0	11-13 12.0	8-12 10.0
apachecus	3.09-3.46 3.327	1.35-1.39 1.363	12-13 12.3	10-16 13.0	0-2 1.0	4-6 5.0	3-4 3.3	11-12 11.3	10-11 10.3
roretzi	3.80-4.03 3.915	1.43-1.50 1.465	11 11.0	6 6.0	4 4.0	11-12 11.5	7 7.0	15 15.0	15 15.0

	CW/CL	AMD/CL	ALS/ALD	SL/SW	IFL/CL	IML/CL	IVMCR
unicolor	0.69-0.79 0.735±.020	0.016-0.025 0.022± .002	1.04-2.55 1.776±.296	1.13-1.27 1.187±.036	0.63-0.76 0.710±.023	0.35-0.48 0.439±.023	6-10 7.7(8)
robustus	0.73-0.79 0.767±.015	0.021-0.024 0.022± .001	1.61-2.75 2.124±.330	1.08-1.16 1.126±.021	0.68-0.72 0.698±.014	0.38-0.42 0.404±.012	6-9 7.3(7)
pacificus	0.71-0.79 0.766±.021	0.015-0.025 0.020± .003	1.37-2.65 1.768±.240	1.13-1.35 1.234±.052	0.71-0.80 0.756±.024	0.42-0.51 0.467±.020	6-9 7.1(7)
pugnax	0.72-0.80 0.765±.023	0.018-0.026 0.022± .002	1.26-2.04 1.607±.232	1.10-1.24 1.169±.031	0.68-0.77 0.721±0.28	0.39-0.48 0.426±.021	6-9 7.5(7)
montanus	0.77-0.85 0.808±.024	0.016-0.023 0.019± .002	1.67-2.63 2.157±.302	1.06-1.18 1.130±.033	0.70-0.79 0.754±.027	0.44-0.52 0.483±.022	6-8 7.3(7)
hageni	0.72-0.79 0.766±.031	0.017-0.020 0.019± .001	1.55-1.90 1.669±.130	1.21-1.37 1.260±.056	0.73-0.77 0.745±.017	0.43-0.48 0.459±.018	6-7 6.6(7)
cerberus	0.77-0.80 0.782	0.016-0.017 0.017	1.77-2.15 1.997	1.15-1.22 1.193	0.76-0.79 0.768	0.43-0.46 0.444	7-9 8.0
yesoensis	0.79	0.020	1.83	1.19	0.71	0.41	6
lincolnianus	0.79-0.82 0.809	0.013-0.016 0.015	1.85-2.27 2.062	1.15-1.20 1.175	0.71-0.73 0.721	0.41-0.42 0.415	8-9 8.5
stygius	0.76-0.77 0.764	0.017-0.020 0.018	1.64-2.70 2.048	1.09-1.12 1.109	0.66-0.69 0.679	0.35-0.38 0.373	6-9 8.0
apachecus	0.78-0.82 0.801	0.016-0.020 0.018	1.22-2.00 1.739	1.14-1.21 1.155	0.71-0.76 0.735	0.40-0.44 0.422	6-9 7.7
roretzi	0.83-0.84 0.834	0.021-0.022 0.021	2.25-2.48 2.367	1.10-1.13 1.119	0.76-0.78 0.775	0.45-0.46 0.453	6-7 6.5

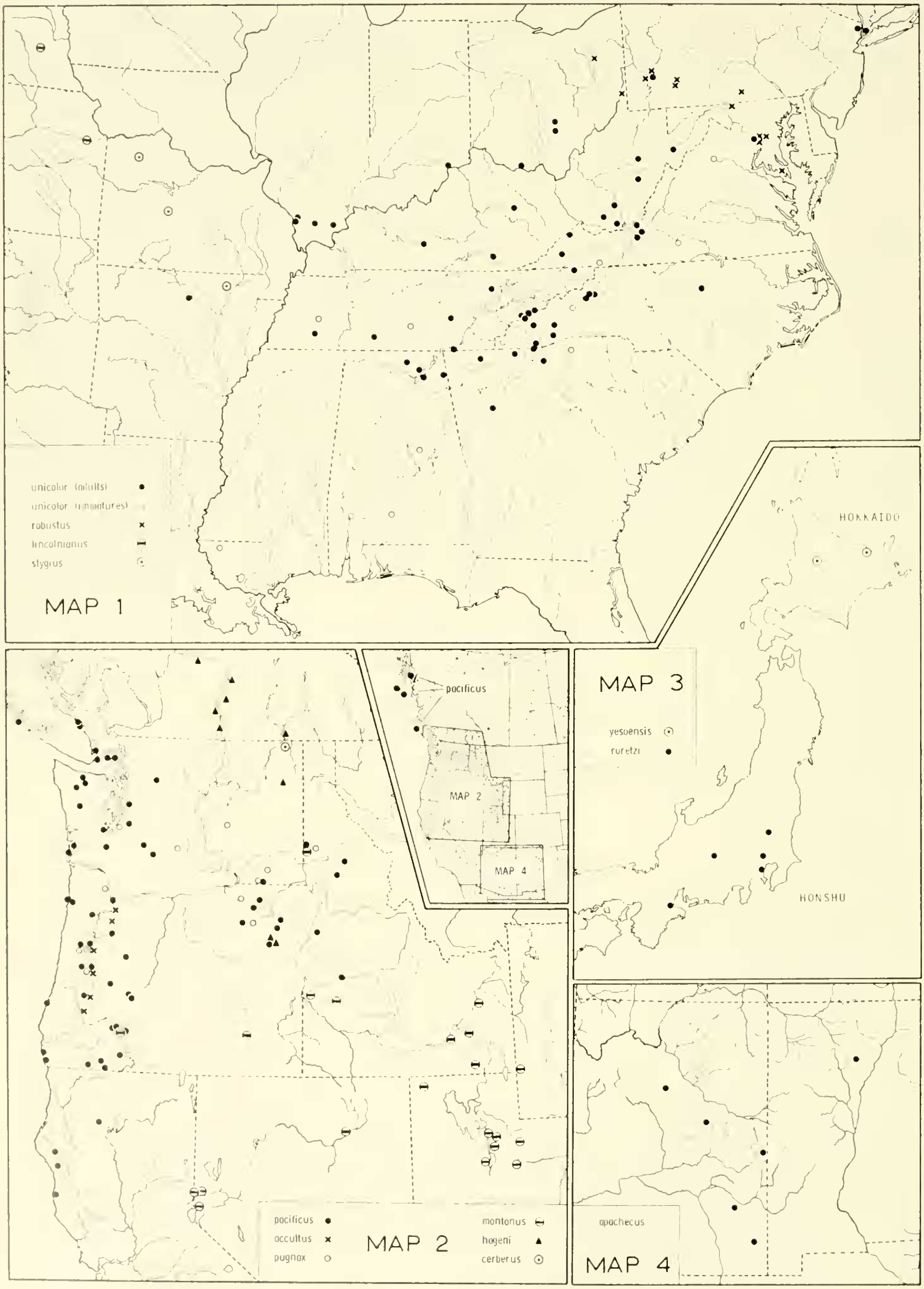
Table 14 (concluded).

	IVTL/CL	IVML/CL	IFL/IML	IFL/IVFL	IVTL/IVTarL	IVML/IVTarL	IVML/IML
unicolor	0.34-0.46 0.403±.022	0.49-0.68 0.596±.040	1.48-1.81 1.620±.059	0.98-1.11 1.030±.026	1.58-1.92 1.783±.093	2.33-3.06 2.632±.142	1.16-1.57 1.358±.063
robustus	0.37-0.39 0.381±.008	0.52-0.57 0.554±.015	1.65-1.78 1.730±.034	1.01-1.05 1.039±.011	1.77-2.02 1.830±.104	2.47-2.81 2.613±.107	1.28-1.41 1.349±.040
pacificus	0.35-0.41 0.388±.015	0.51-0.65 0.582±.033	1.50-1.69 1.618±.050	1.04-1.17 1.105±.036	1.60-1.85 1.706±.072	2.38-2.79 2.558±.119	1.09-1.38 1.247±.066
pugnax	0.37-0.43 0.404±.017	0.56-0.65 0.601±.026	1.60-1.74 1.693±.037	1.00-1.10 1.044±.021	1.52-1.74 1.663±.054	2.26-2.70 2.474±.101	1.31-1.50 1.413±.059
montanus	0.40-0.48 0.429±.021	0.60-0.65 0.639±.016	1.48-1.61 1.562±.041	1.00-1.07 1.035±.018	1.58-2.16 1.953±.156	2.40-3.18 2.912±.224	1.24-1.39 1.324±.046
hageni	0.41-0.43 0.428±.088	0.61-0.65 0.638±.015	1.58-1.68 1.623±.035	1.00-1.03 1.014±.011	1.81-2.08 1.889±.104	2.59-2.92 2.814±.070	1.31-1.46 1.391±.060
cerberus	0.42-0.44 0.431	0.62-0.67 0.645	1.70-1.75 1.728	1.04-1.07 1.057	1.93-2.10 1.992	2.84-3.15 2.983	1.44-1.47 1.453
yesoensis	0.39	0.56	1.71	1.02	1.75	2.54	1.35
lincolnianus	0.38-0.39 0.390	0.56 0.567	1.73-1.74 1.738	1.04-1.08 1.061	1.75-1.84 1.798	2.56-2.66 2.613	1.35-1.38 1.367
stygius	0.35-0.38 0.364	0.48-0.53 0.514	1.79-1.86 1.819	1.04-1.05 1.046	1.81-1.88 1.846	2.54-2.70 2.607	1.36-1.38 1.376
apachecus	0.35-0.45 0.371	0.50-0.54 0.522	1.70-1.80 1.743	1.09-1.13 1.116	1.67-1.78 1.731	2.29-2.54 2.440	1.21-1.26 1.239
roretzi	0.37-0.39 0.383	0.57-0.58 0.578	1.71 1.713	1.05-1.07 1.060	1.73-1.81 1.770	2.66-2.68 2.672	1.27 1.277

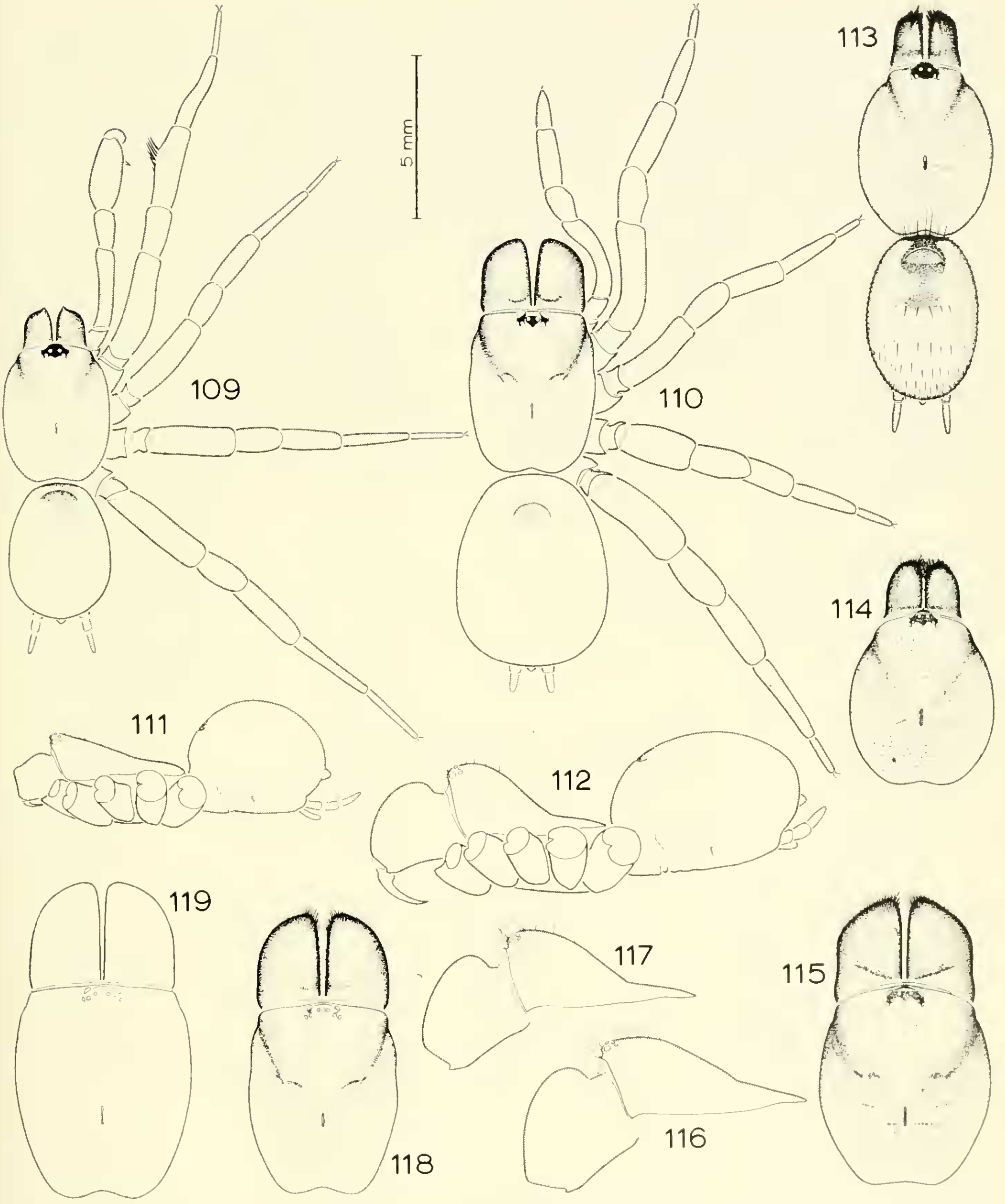
TABLE 15. MEASUREMENTS (IN MM) AND MERISTIC CHARACTER VALUES FOR HOLOTYPE AND LECTOTYPE SPECIMENS OF *ANTRODIAETUS* SPECIES.

Leg IV segments distal of femur missing on *A. robustus* lectotype. Pedipalp segments flattened out of shape on *A. lincolnianus* holotype. * MM is metarsus I macrosetae pattern; TP is number of macrosetae (total, ensiform) on prolateral surface of tibia I; and TRV is number of macrosetae (total, ensiform) on retrolateral aspect of ventral surface of tibia I.

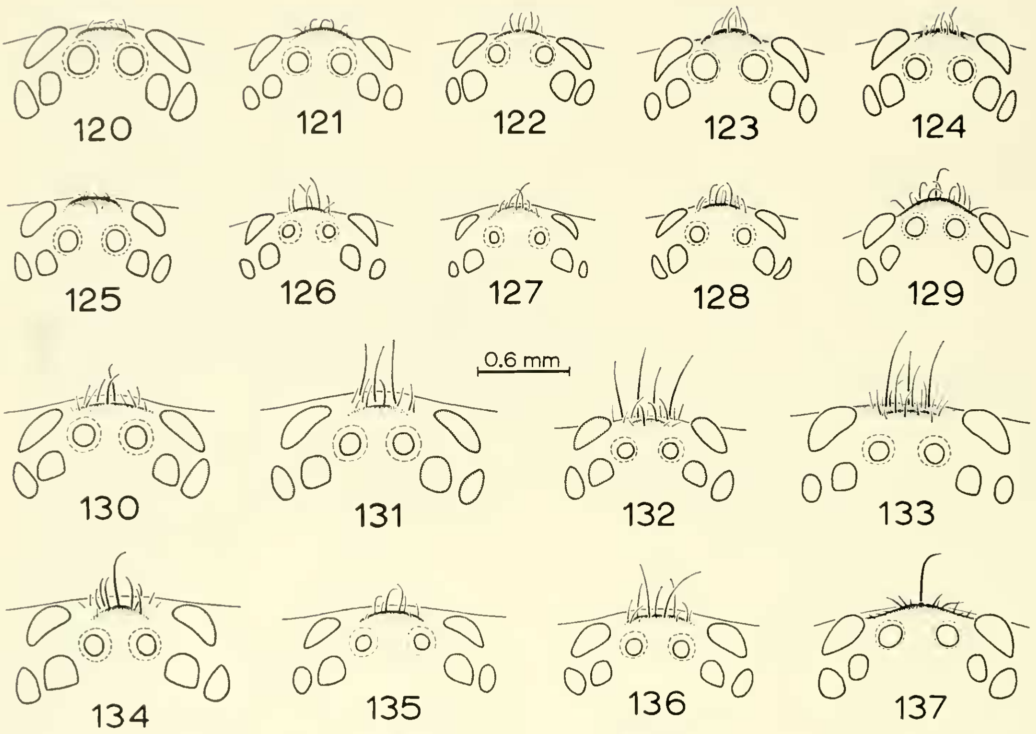
	robustus	*pacificus*	*occultus*	*montanus*	*hageni*	*cerberus*	*lincolnianus*	*stygius*	*apachecus*
CL	6.95	5.34	5.57	5.27	6.17	5.19	5.12	4.66	4.66
CW	5.48	4.33	4.56	4.48	5.16	4.22	4.22	3.54	3.73
OQW	1.44	1.03	1.12	1.03	1.08	0.93	0.90	0.91	0.86
ALS	0.75	0.51	0.51	0.57	0.57	0.47	0.44	0.45	0.43
ALD	0.35	0.31	0.35	0.29	0.33	0.25	0.23	0.25	0.25
AMS	0.21	0.14	0.14	0.18	0.18	0.16	0.22	0.20	0.17
AMD	0.17	0.14	0.16	0.14	0.12	0.09	0.07	0.11	0.09
SL	3.78								
SW	3.44								
IFL	4.88	4.71	4.97	5.46	5.61	5.05	4.90	4.63	4.41
ITL	2.80	3.01	3.31	3.77	3.95	3.35	3.58	3.20	3.09
IML	2.83	4.22	3.84	4.29	4.37	3.58	3.54	3.50	3.16
ITarL	1.40	1.96	2.33	2.63	2.71	2.03	1.92	2.18	1.80
IVFL	4.69								
PFL		3.54	3.39	3.65	3.92	3.12		3.61	3.54
PTL		2.94	3.01	3.12	3.54	2.56		3.09	2.94
PTT		1.23	1.38	1.20	1.40	1.01		0.98	0.96
EGS		36	25		59	46		31	69
CT	12								
CMT	12								
PTSP	6								
PTSR	3								
IMS	10								
*MM		none	none	A	AB	AB	AB	A	A
*TP		38,0	35,16	35,27	44,44	17,16			
*TRV		6,0	4,2	18,13	12,12	6,6			

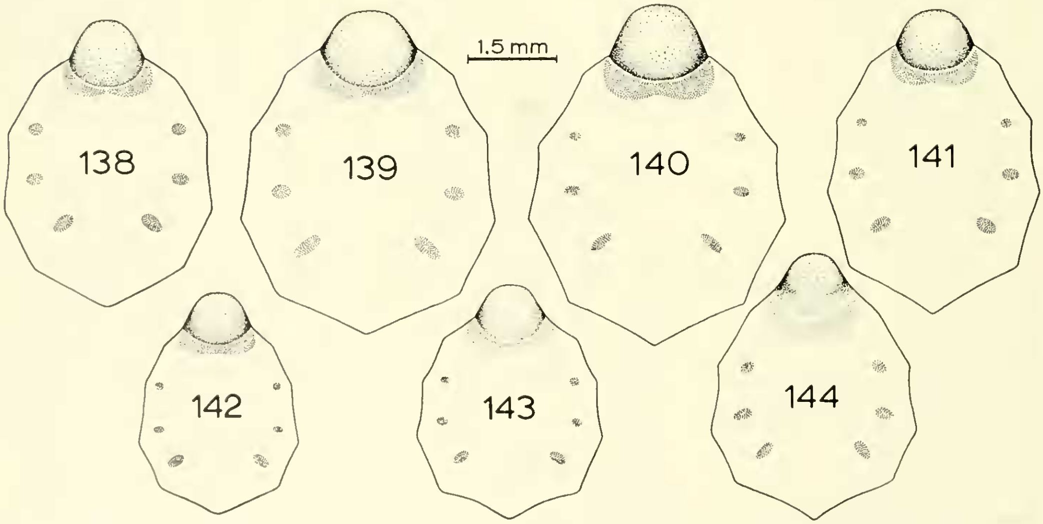


Maps 1–4. Distribution of *Antrodiaetus* species.

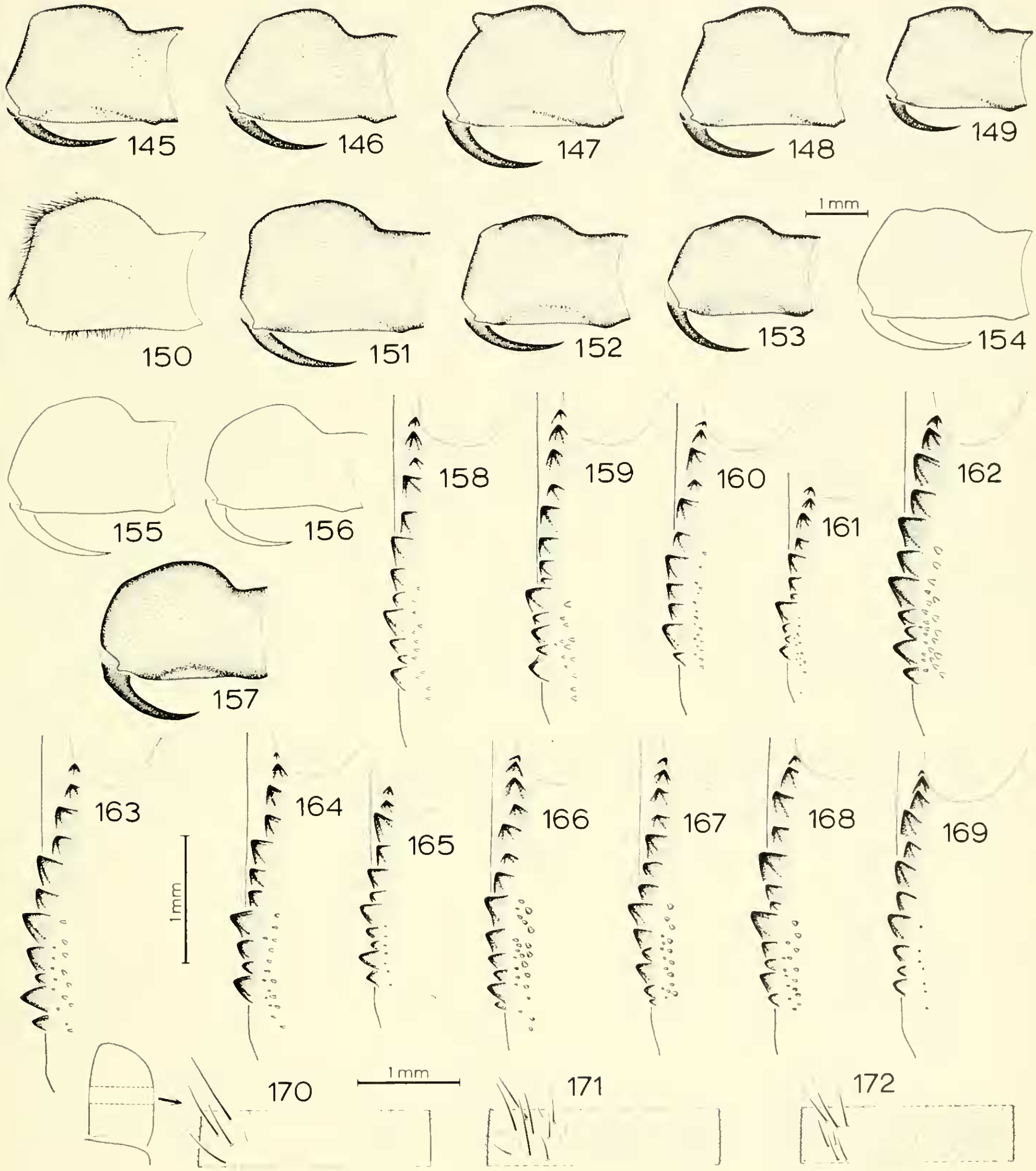


Figures 109–119. Whale body and carapace views of *Antrodiaetus*. (Dorsal and lateral views.) 109–112. *A. pugnax*, *B.* 109. Male. 110. Female. 111. Male. 112. Female. 113. *A. unicolor* male, *I.* 114–116. *A. roretzi*. 114. Male. 115–116. Female. 117–118. *A. stygius* paratype female. 119. *A. lincolnianus* female; Lincoln, Nebr.

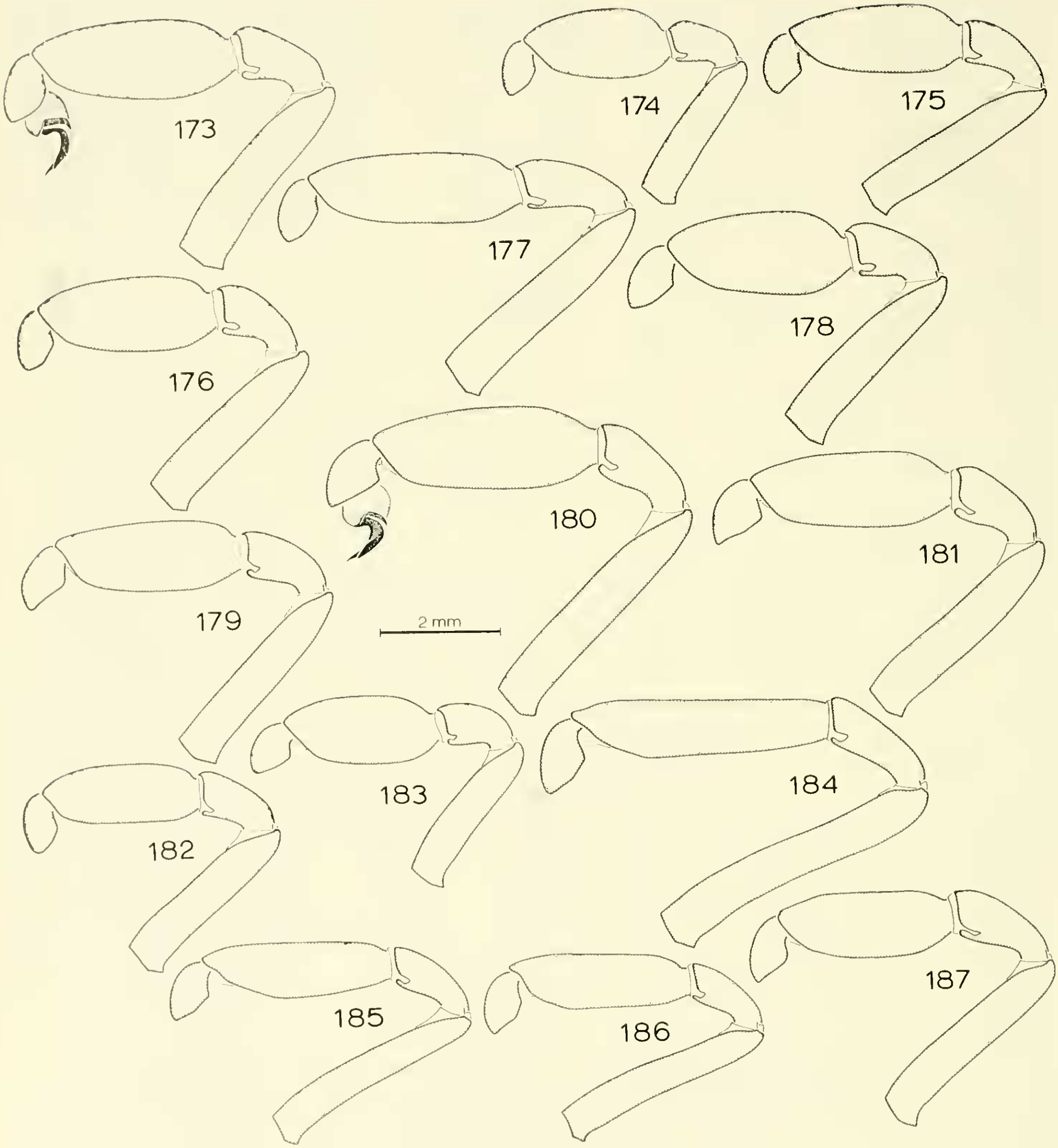




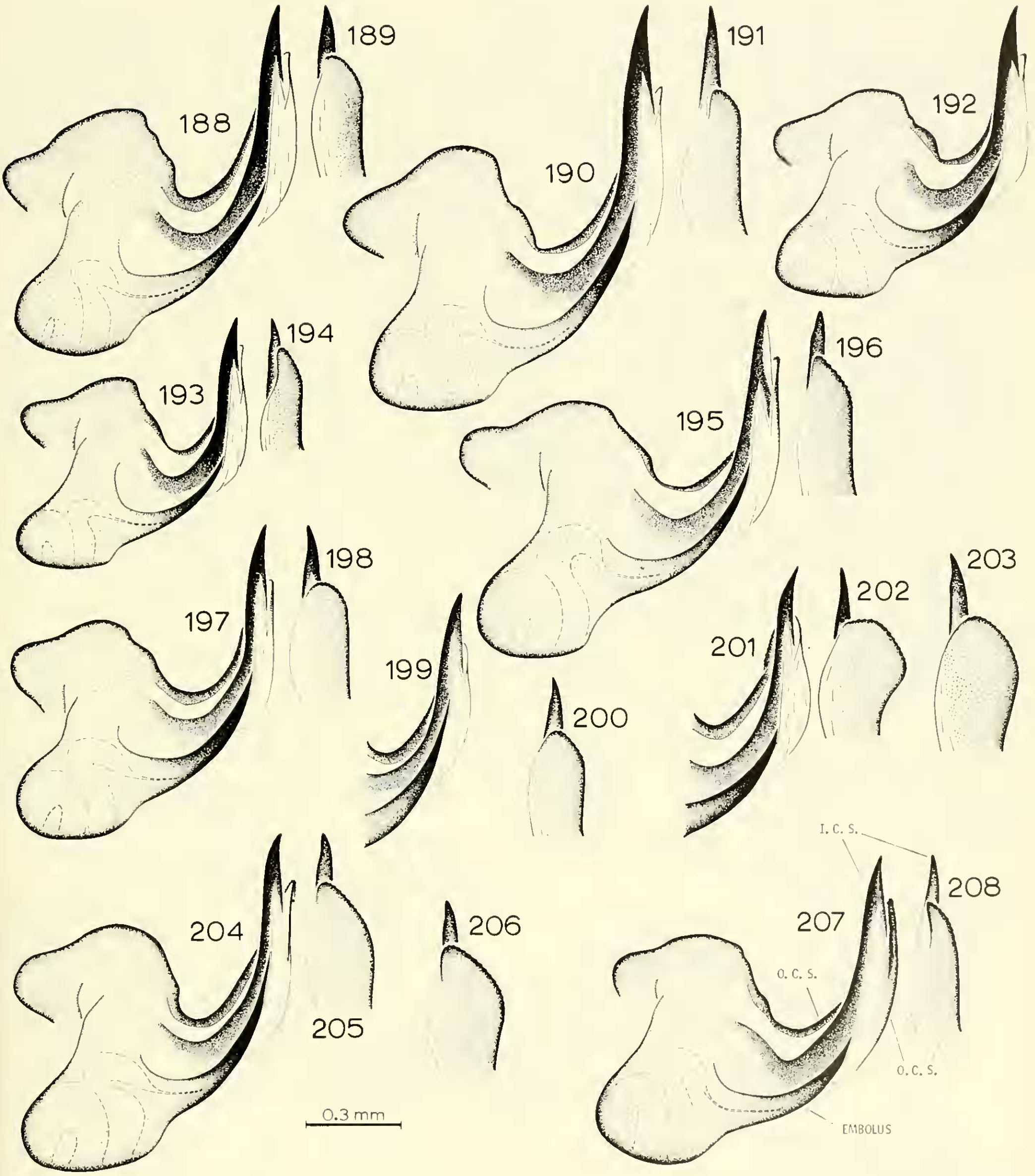
Figures 120–137. *Antrodiaetus* eyes. (Dorsal view with lateral border of carapace horizontal.) 120–129. Males. 120. *A. unicolor, P.* 121–122. *A. pacificus.* 121. Holotype. 122. *R.* 123. *A. occultus*, paratype. 124. *A. pugnax, A* (*Brachybothrium shoshoneum* Chamb., holotype). 125. *A. hageni*; near Baker, Ore. 126. *A. cerberus*, holotype. 127. *A. lincolnianus*, holotype. 128. *A. stygius*, holotype. 129. *A. roretzi*, Saitama Pref. 130–137. Females. 130. *A. unicolor, P.* 131. *A. pacificus, L.* 132. *A. pugnax, B.* 133. *A. hageni*; Trail, B. C. 134. *A. cerberus*, paratype. 135. *A. lincolnianus*; Lincoln, Nebr. 136. *A. stygius*, paratype. 137. *A. roretzi.* Figures 138–144. Sternum and labium of *Antrodiaetus* females. 138. *A. unicolor, Q.* 139. *A. robustus*; Canton, Ohio. 140. *A. montanus*; Salt L. City, Utah. 141. *A. hageni*; Kelowna, B. C. 142. *A. yesoensis.* 143. *A. stygius*, paratype. 144. *A. roretzi*, Tochigi Pref.



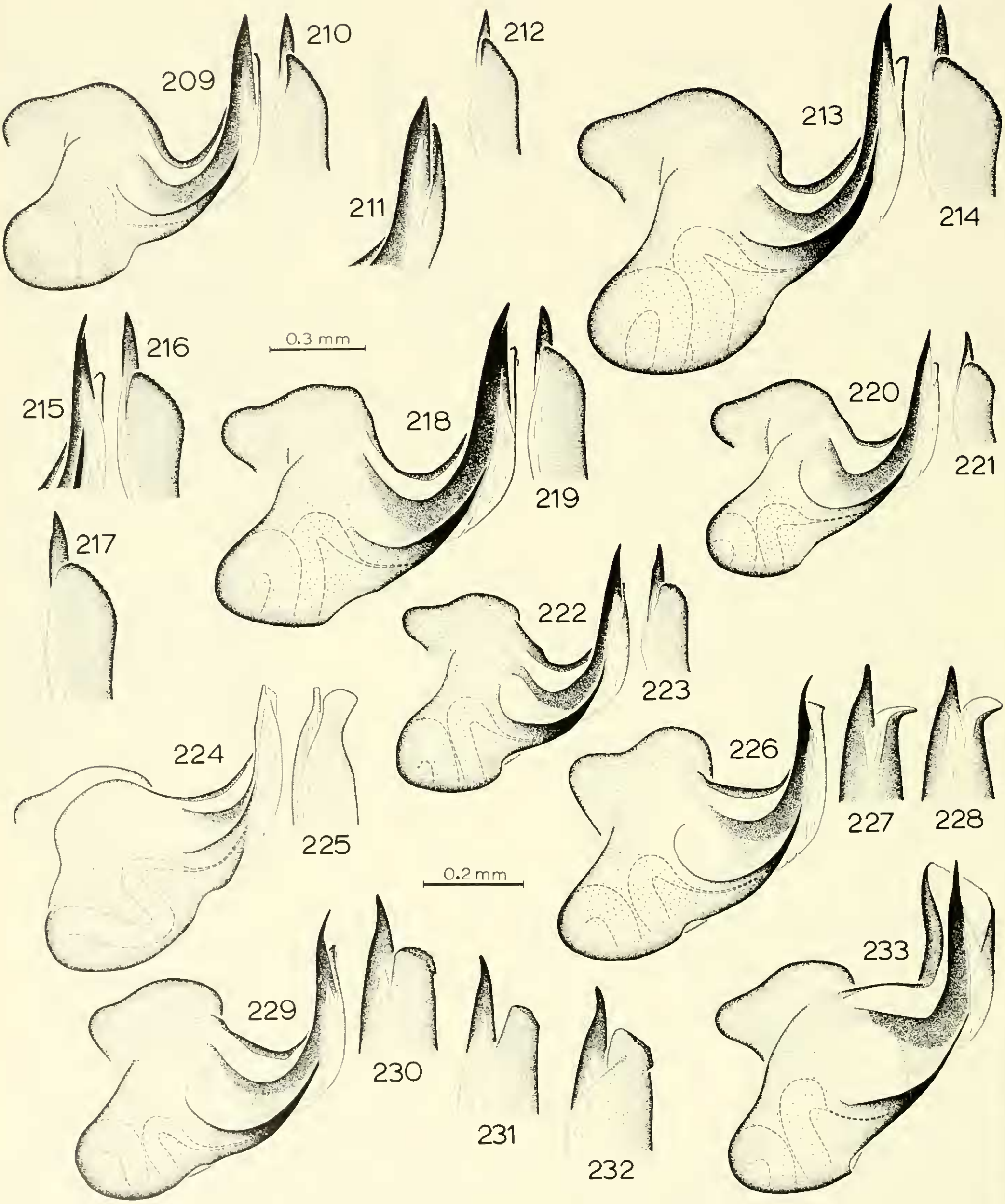
Figures 145–157. Chelicerae of *Antrodiaetus* males. (Retrolateral view of left chelicera.) 145–146. *A. unicolor*. 145. *F*. 146. *B*. 147–149. *A. pacificus*. 147. *B*. 148. *F*. 149. *D*. 150. *A. montanus*; Idaho Falls, Ida. 151. *A. hageni*; Baker, Ore. 152. *A. lincolnianus*, paratype. 153. *A. stygius*, holotype. 154–156. *A. apachecus*. 154–155. Near Alpine, Ariz. 156. Paratype. 157. *A. roretzi*, Yokohama. Figures 158–169. Cheliceral teeth of *Antrodiaetus* females. (Ventral view of left chelicera.) 158. *A. unicolor*, *J*. 159. *A. robustus*; Hagerstown, Md. 160. *A. pacificus*, *L*. 161. *A. pugnax*, *B*. 162. *A. montanus*; Downey, Ida. 163. *A. hageni*; Kelowna, B. C. 164. *A. cerberus*, paratype. 165. *A. yesoensis*. 166. *A. lincolnianus*; Lincoln, Nebr. 167. *A. stygius*, paratype. 168. *A. apachecus*; Flagstaff, Ariz. 169. *A. roretzi*; Tochigi Pref. Figures 170–172. Setation of upper ectal surface of *Antrodiaetus* female chelicerae. (Dorsal view.) 170. *A. pacificus*, *L*. 171. *A. montanus*; Downey, Ida. 172. *A. hageni*; Trail, B. C.



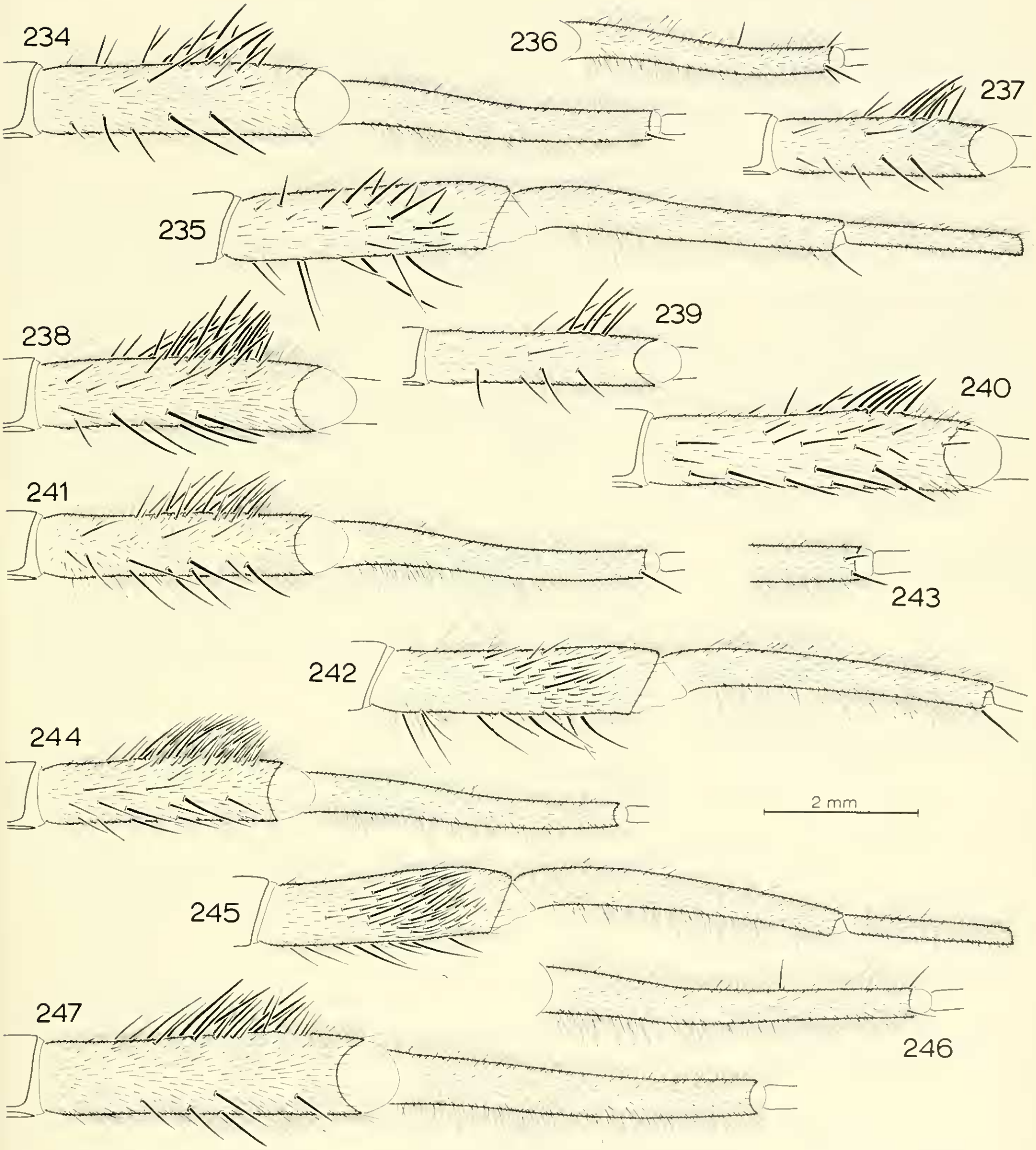
Figures 173–187. *Antrodiaetus* male pedipalps. (Retrolateral view of left pedipalp.) 173–174. *A. unicolor.* 173. Q. 174. N. 175–177. *A. pacificus.* 175. D. 176. B. 177. J. 178. *A. occultus,* paratype. 179. *A. pugnax,* A (*Brachybothrium shoshoneum* Chamb. holotype). 180. *A. montanus;* Idaho Falls, Ida. 181. *A. hageni;* Summerland, B. C. 182. *A. cerberus,* holotype. 183. *A. yesoensis.* 184. *A. lincolnianus;* Lawrence, Kan. 185. *A. stygius,* holotype. 186. *A. apachecus,* holotype. 187. *A. roretzi,* Saitama Pref.



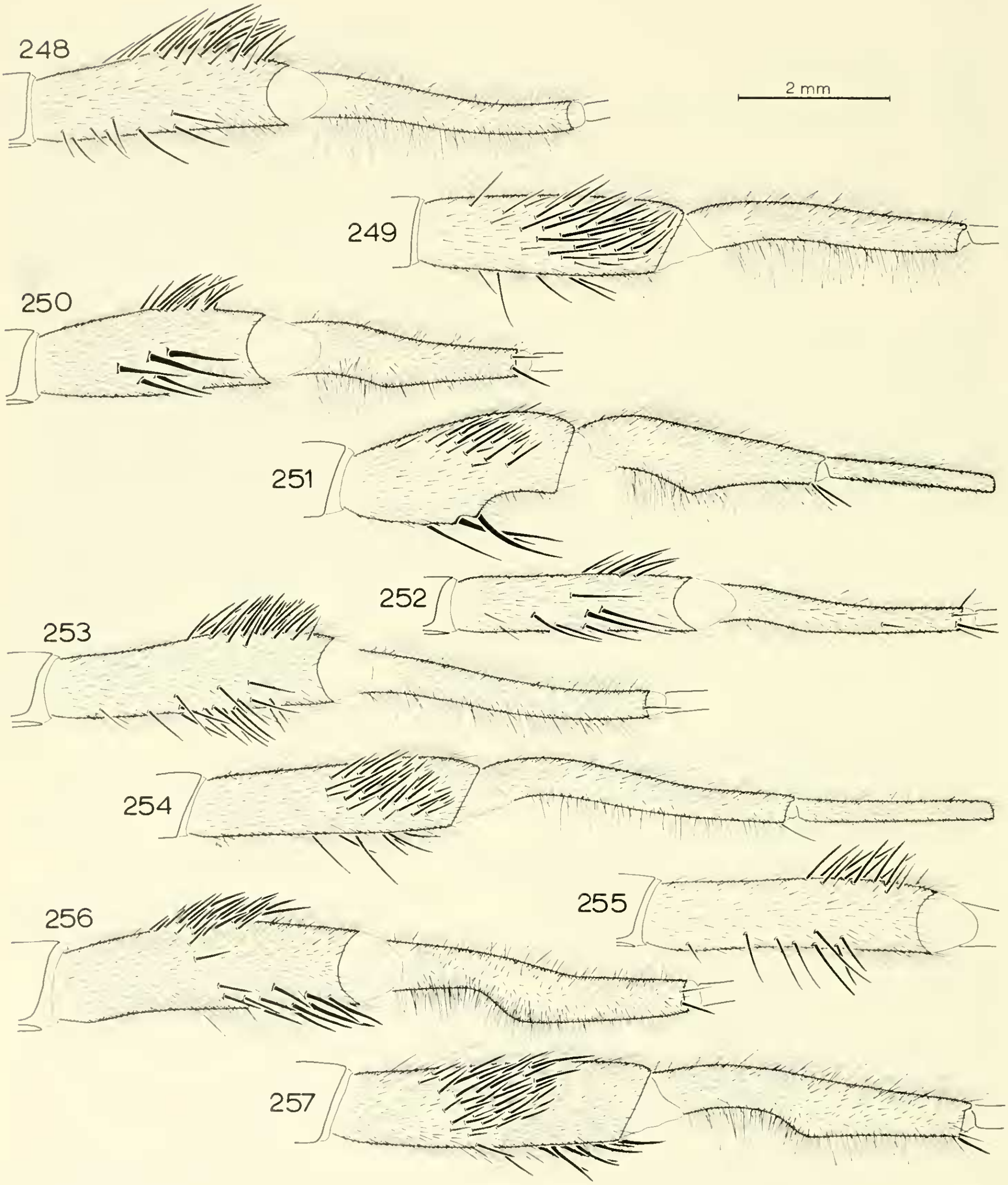
Figures 188–208. *Antrodiaetus* palpi. (Prolateral view of entire left palpus and view of tip after palpus rotated 90° on longitudinal axis of distal half of i.c.s. Occasionally prolateral view does not include bulb portion of palpus.) 188–194. *A. unicolor*. 188–189. *Q*. 190–191. *B*. 192. *N*. 193–194. *A*. 195–196. *A. robustus*; near Washington, D. C. (*Brachybothrium shoemakeri* Petrunk., lectotype). 197–203. *A. pacificus*. 197–198. *D*. 199. Holotype. 200. Ketchikan, Alaska. 201–202. *S*. 203. *W*. 204–206. *A. accultus*. 204–205. Holotype. 206. Yoncalla, Ore. 207–208. *A. pugnax*, *A* (*Brachybothrium shoshoneum* Chamb. holotype).



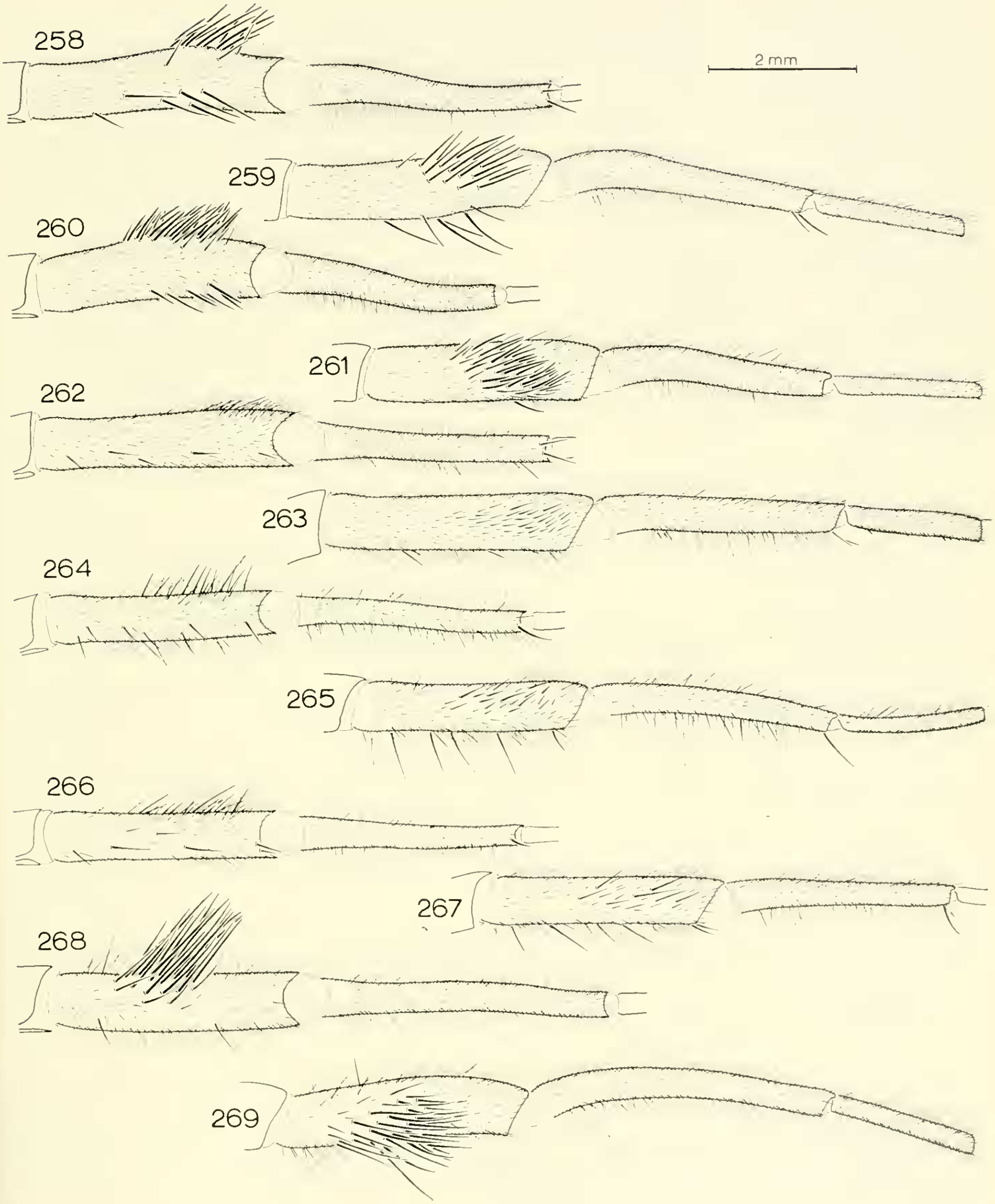
Figures 209–233. *Antrodiaetus* palpi. (Same views as previous plate. Figs. 225, 227–228, and 230–232 enlarged; match 0.2 mm scale.) 209–212. *A. pugnax.* 209–210. *H.* 211. *C.* 212. *E.* 213–217. *A. montanus.* 213–214. Paratype; Notus, Ida. 215–216. Fish Lake, Ore. 217. Washoe Valley, Nev. 218–219. *A. hageni*, holotype. 220–221. *A. cerberus*, holotype. 222–223. *A. yesaensis.* 224–225. *A. lincolnianus*, paratype. 226–228. *A. stygius.* 226–227. Holotype. 228. Paratype. 229–232. *A. apachecus.* 229–230. Paratype. 231. Near La Cueva, N. Mex. 232. Near Alpine, Ariz. 233. *A. roretzi*, Saitama Pref.



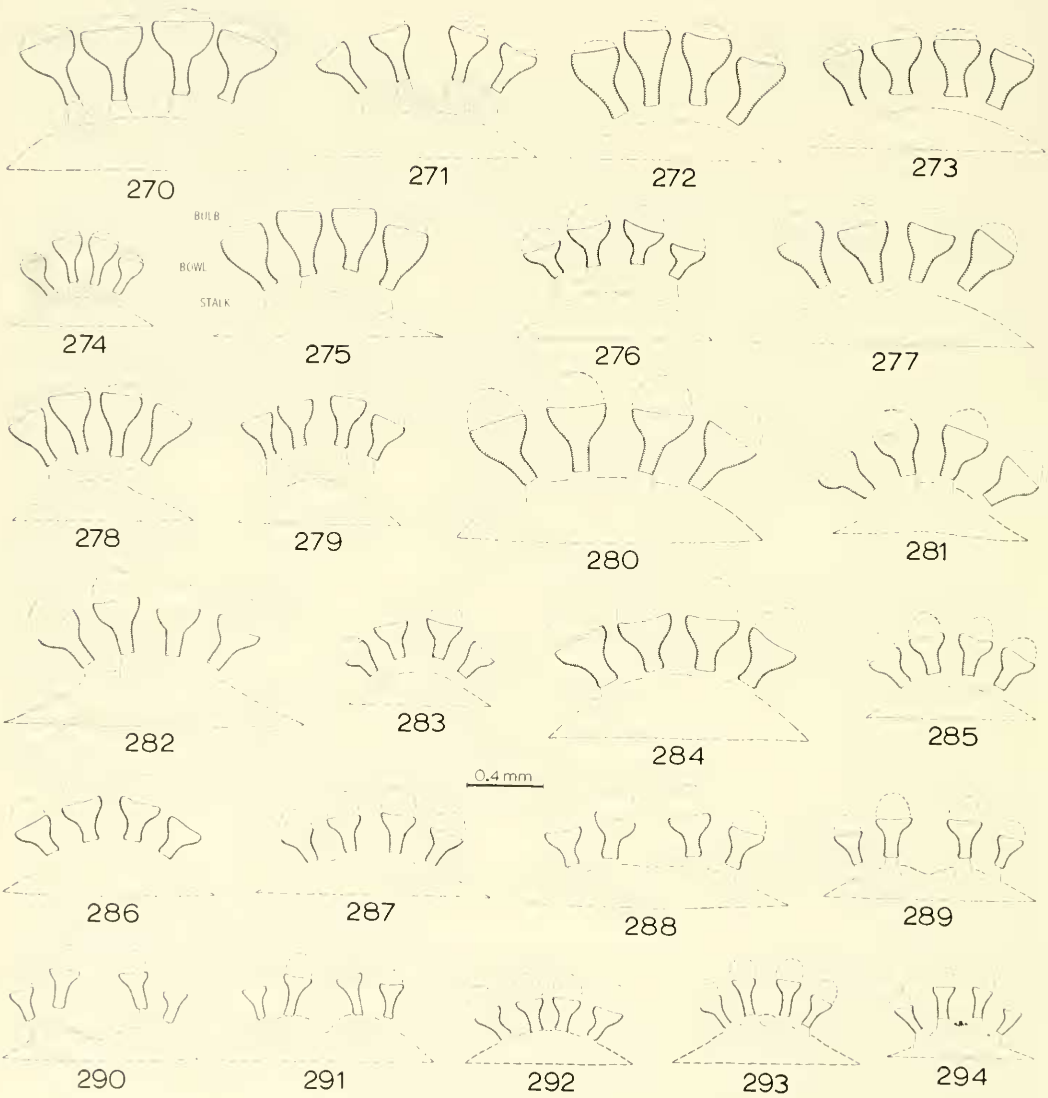
Figures 234–247. Tibia, metatarsus, and tarsus of leg I of *Antrodiaetus* males. (Ventral and prolateral views of left leg.) 234–240. *A. unicolor*. 234–235. *P*. 236. *F*. 237. *A*. 238. *I*. 239. *N*. 240. *Q*. 241–243. *A. robustus*. 241–242. Near Rector, Pa. 243. Distal end of metatarsus (ventral view), near Rector. 244–247. *A. pacificus*. 244–245. *D*. 246. *T*. 247. *W*.



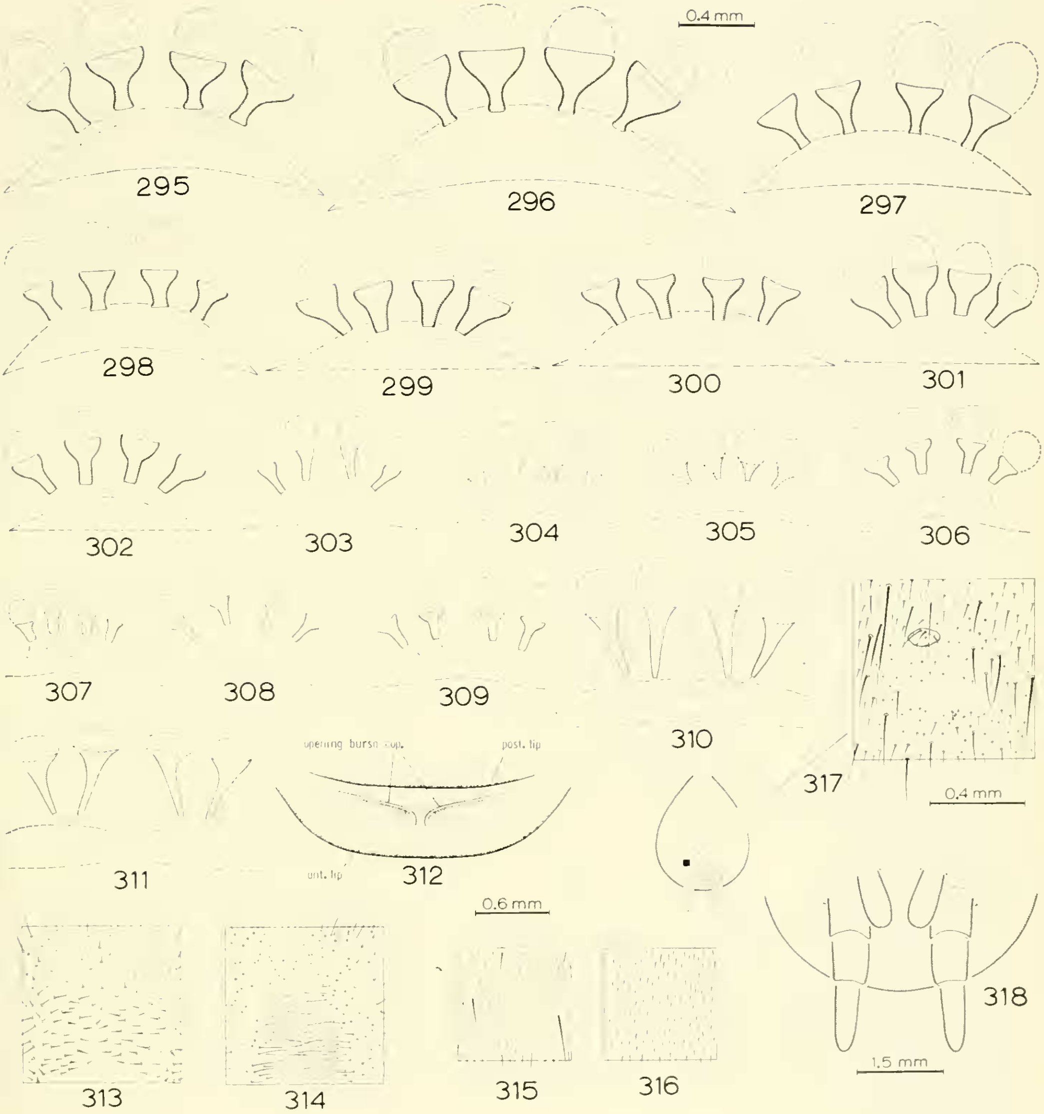
Figures 248–257. Tibia, metatarsus, and tarsus of leg I of *Antrodiaetus* males. (Ventral and prolateral views of left leg.) 248–249. *A. occultus*, holotype. 250–252. *A. pugnax*. 250–251. *A* (*Brachybothrium shoshoneum* Chamb. holotype). 252. *H.* 253–255. *A. montanus*. 253–254. Holotype. 255. Paratype; Strawberry Reservoir, Ida. 256–257. *A. hageni*, holotype.



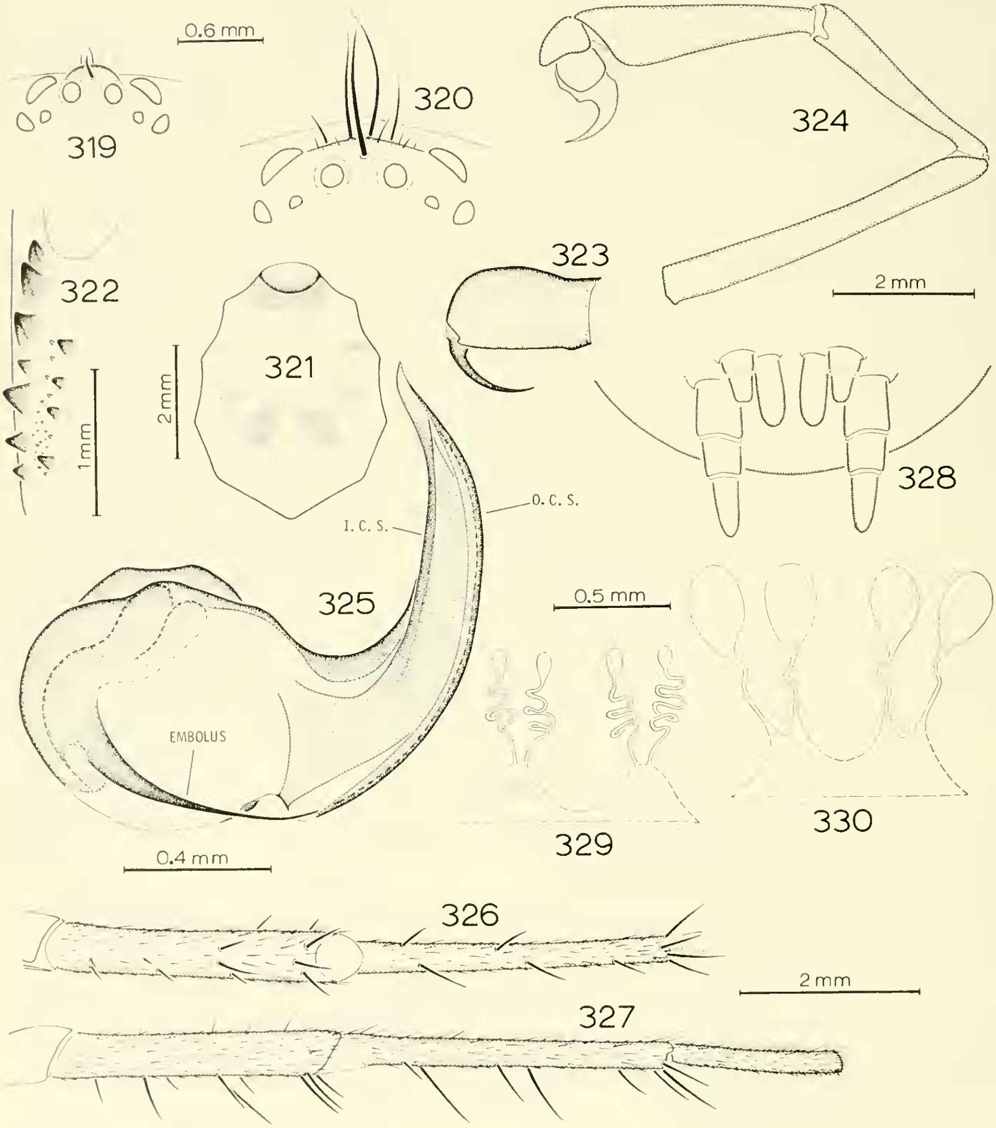
Figures 258–269. Tibia, metatarsus, and tarsus of leg I of *Antrodiaetus* males. (Ventral and prolateral views of left leg.) 258–259. *A. cerberus*, holotype. 260–261. *A. yesaensis*. 262–263. *A. lincolnianus*, paratype. 264–265. *A. stygius*, paratype. 266–267. *A. apachecus*, holotype. 268–269. *A. roretzi*; Yokohama.



Figures 270–294. *Antrodioetus* seminal receptacles. (Dorsal view. Floor of bursa copulatrix outlined by broken line.) 270–279. *A. unicolor*. 270. *J*. 271. *C*. 272. *K*. 273. *I*. 274–275. Q. 276. *B*. 277. *K*. 278. *F*. 279. O. 280–283. *A. robustus*. 280. Baldwin, Pa. 281. Hagerstown, Md. 282. Canton, Oh. 283. Caledonia St. Pk., Pa. 284–291. *A. pacificus*. 284. Brookings, Ore. 285. *I*. 286. *M*. 287. Queen Charlotte Islands, B. C. 288–290. *S*. 291. *Y* (Kamiah). 292–294. *A. pugnax*. 292. Fort Lewis, Wash. 293. *B*. 294. Lewis and Clark St. Pk., Wash.



Figures 295–311. *Antrodiaetus* seminal receptacles. (Dorsal view. Floor of bursa copulatrix outlined by broken line.) 295–298. *A. montanus*. 295. Reno, Nev. 296. Pocatello, Ida. 297. Salt L. City, Utah. 298. Downey, Ida. 299–300. *A. hageni*. 299. Kelowna, B. C. 300. Kamloops, B. C. 301–302. *A. cerberus*, paratypes. 303. *A. yesoensis* (likely immature). 304–305. *A. lincolnianus*; Lincoln, Nebr. 306–307. *A. stygius*; paratypes. 308–309. *A. apachecus*. 308. Flagstaff, Ariz. 309. Paratype. 310–311. *A. roretzi*. 311. Tochigi Pref. Figure 312. *A. roretzi*. Posterior ventral view of exterior surface of female genitalia. Figures 313–318. External morphology of female *Antrodiaetus* abdomen. 313–314. Setation medially and dorsally just posterior of pedicel. 313. *A. unicolor*, P. 314. *A. robustus*; Baldwin, Pa. 315–316. Dorsal abdominal background setation (1 mm post. of tergite). 315. *A. unicolor*, P. 316. *A. robustus*; Baldwin, Pa. 317. *A. robustus*, AL spinneret vestige. 318. *A. unicolor* spinnerets, O. 0.6 mm scale for 312–316.



Figures 319–330. *Aliatypus* morphology. (Same views as for *Antrodiaetus*.) 319–329. *Aliatypus* no. 2; Chatsworth, Calif. 319. Male eyes. 320. Female eyes. 321. Female sternum. 322. Female cheliceral teeth. 323. Male chelicera. 324. Male pedipalp. 325. Palpus. 326–327. Distal segments of male leg I. 328. Female spinnerets. 329. Seminal receptacles. 330. *Aliatypus* sp.; Shaver Lake (Fresno Co.), Calif. Seminal receptacles. 319–320: 0.6 mm scale. 321: 2 mm scale. 322: 1 mm scale. 323–324, 328: 2 mm scale. 325: 0.4 mm scale. 326–327: 2 mm scale. 329–330: 0.5 mm scale.

EVOLUTION

PHYLOGENY

Atypoidea. Simon (1892) first emphasized the close relationship of the Antrodiaetidae, the Mecicobothriidae, and the Atypidae, but later (1903), impressed by the resemblance of the first two families to the ctenizids and diplurids, he separated these from the atypids and grouped them with the rest of the mygalomorph spiders. Smith (1908) studied *Atypoides* and *Aliatypus* and sided with Simon's earlier opinion. However, until the 1940's, many authors accepted Simon's second classification uncritically. Chamberlin and Ivie (1945) pointed out that the similarities of the antrodiaetids to the ctenizids and of the mecicobothriids to the diplurids were the result of convergence. Gertsch (1949, 1967) agreed, and grouped the Antrodiaetidae, Mecicobothriidae, and Atypidae together with the Liphistiidae to form the superfamily Atypoidea and to emphasize their close relationship and their distinctness from other mygalomorph taxa.

Evidence strongly indicates that the antrodiaetids, mecicobothriids, and atypids do form a distinct and monophyletic group. The homogeneity of genital structure within this group and the distinctness of the genitalia from those of nonatypoid taxa is perhaps the strongest indication of this monophyly; the genitalia are relatively complex structures probably not strongly affected by niche-oriented convergence. The always well-developed o.c.s. (Fig. 207) and the frequently present i.c.s. are absent from all nonatypoid palpi, and the Atypoidea possess four seminal receptacles (or a condition derived from this) rather than the usual two (or a derived condition) of other mygalomorphs. Other characters providing similar evidence are listed by Chamberlin and Ivie (1945). It is certain that the Antrodiaetidae are phylogenetically quite distinct from the ctenizids and that the similarity of their niches, together with a large number of functionally related (niche adapted) morphological and behavioral similarities, is simply the result of convergent, or at least parallel, evolution.

The unique ancestral characters (vestiges of abdominal segmentation) shared by the antrodiaetids, mecicobothriids, and atypids indicate a long evolutionary history for this group. Each of these families is distinct and contains few species—these are truly evolutionary relicts. The family Atypidae is highly specialized morphologically and behaviorally in accord with the unique tube-web niche which it has entered. The mecicobothriids apparently occupy a distinct sheet-web niche and are morphologically more similar to the antrodiaetids (not necessarily more closely related) than to the atypids.

Antrodiaetidae. The evidence summarized in Table 11 shows that *Aliatypus* arose from an ancestral stock distinct from that of *Antrodiaetus* and *Atypoides*, and also that *Aliatypus* may be as closely or more closely related to the Mecicobothriidae. Smith (1908) arrived at a somewhat similar conclusion. The first two characters (Table 11), which are heavily weighted for reasons given earlier, indicate that *Aliatypus* is more closely related to the mecicobothriids. Characters 3 to 5 probably compose a complex of characters functionally related to mating behavior and therefore are individually less heavily weighted. These provide only weak evidence that *Aliatypus* may be more closely related to the mecicobothriids. Some, perhaps even all, of the last nine characters are functionally correlated with the niche requirements of these taxa and therefore may be misleading. Although the trapdoor niche of *Aliatypus* is much more similar to (but still different from) the niche of *Antrodiaetus* and *Atypoides* than to the nonburrowing sheet-web niche of the mecicobothriids, the genital character evidence and the other distinct character states indicate that this is the result of either parallel or convergent evolution. A complete study of the

Table 11. Comparison of *Aliatypus* with related taxa. Thickness of arrows is roughly proportional to weight of character and degree of similarity of character states. *Hexura picea* (♂, ♀) and *Megahexura fulva* (♀) are the only mecicobothriids examined.

CHARACTER	*Antrodiaetus* & *Atypoides*		*Aliatypus*		Mecicobothriidae
1. Palpus form	distinct		similar to *Hexura*	↔	similar to *Aliatypus*
2. Seminal receptacle form	stalk moderately to well sclerotized, rarely sinuous, usually with bowl		stalk unsclerotized, very narrow, sinuous, without bowl	↔	stalk rather weakly sclerotized, narrow, sometimes sinuous, without bowl
3. Male chelicera	apophysis or anterior-dorsal prominence		unmodified	↔	unmodified
4. Male leg I modified	usually		no		yes
5. Male pedipalp patella	not elongate		elongate		not elongate
6. Burrow entrance structure	collar	↔	trapdoor		no burrow (sheet web)
7. Female rastellum	yes	↔	yes		no
8. Pars cephalica	strongly elevated	↔	strongly elevated		weakly elevated
9. Thoracic groove	longitudinal		pit, depression, or absent		longitudinal
10. No. of macroteeth rows per chelicera	1		2		1
11. Metatarsus IV trichobothria number	many		1 (rarely 1-4)		many
12. Large median seta just ant. to AME's	no		yes		no
13. AL spinnerets	absent or non-segmented and degenerating		2-segmented and functional	↔	functional and 1- or 2-segmented
14. Length of labium and inclination to plane of sternum	relatively long, weakly inclined		moderately short, strongly inclined	↔	short, strongly inclined

mecicobothriids and consideration of additional characters are required to clarify the relationships of *Aliatypus*.

Antrodiaetus and *Atypoides* together form a distinct monophyletic group. They are similar to each other in most of the Table 11 characters as well as many others, and are distinct from other related taxa in numerous characters. They differ from one another in two characters: the presence of AL spinnerets and of the male cheliceral apophysis. The former structures are clearly degenerating in *Atypoides* and could possibly have been independently lost more than once. The cheliceral apophysis is not degenerating in *Atypoides*. However, all *Antrodiaetus* males possess an anterior-dorsal cheliceral prominence which, because of its identical location, is more likely homologous to the cheliceral apophysis than independently evolved. That this prominence is probably either of low functional importance or a nonfunctional vestige is perhaps weakly indicated by the high intrapopulation variability of its form in at least some *Antrodiaetus* species. I shall tentatively assume the presence of a functional cheliceral apophysis in the ancestral *Antrodiaetus-Atypoides* stock.

Antrodiaetus consists largely of two distinct but similar species groups each clearly monophyletic and together forming a monophyletic group distinct from *Atypoides.* The *unicolor* group, consisting of nine closely related species, has evolved strongly modified male first legs. The *lincolnianus* group consists of three species, two of which (*A. stygius* and *A. apachecus*) are clearly cognate species. It is probable that this group has undergone a partial reduction in male leg I mating modifications and a functionally related elongation of the male pedipalp, a change convergent to the condition in *Aliatypus.*

Antrodiaetus roretzi, provisionally placed in this genus, is clearly distinct from these two species groups in several characters, the most important being the male palpus structure, female genital structure, and sternum form. It is distinct from *Atypoides* in the latter two characters. It also lacks a cheliceral apophysis and AL spinnerets, but these are probably rather easily lost structures of low reliability. The o.c.s. of the important male palpus is strikingly similar to that of *Atypoides*, but the i.c.s. base has one arm heavily sclerotized as in the other *Antrodiaetus* species, not as in *Atypoides.* The palpus is somewhat distinct in other difficult-to-describe features from all species in both genera. *A. roretzi* is apparently a relict combining some features of both genera; probably its ancestors branched off from or near the *Antrodiaetus-Atypoides* ancestral stock.

Atypoides is a small, rather heterogeneous taxon of three morphologically and behaviorally quite distinct species, each apparently an evolutionary relict. *A. gertschi* is particularly divergent in some characters—seminal receptacle form, male leg I macrosetation, o.c.s. length, male pedipalp shape, and burrow entrance structure. The first three characters bear noteworthy resemblance to *Aliatypus.*

Figure 69 summarizes what I believe to be one of the most probable interpretations of *Antrodiaetus* and *Atypoides* phylogeny, given the present evidence. It is a working hypothesis hopefully of some predictive value.

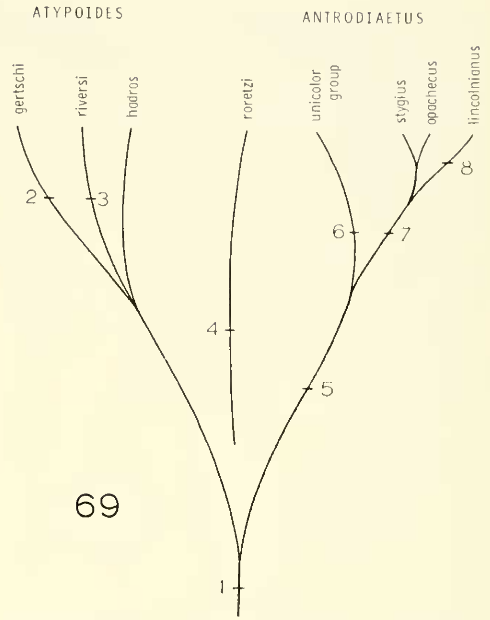


Figure 69. Diagrammatic representation of probable phylogeny of *Antrodiaetus* and *Atypoides*. Some of the more important and likely evolutionary events are indicated. Vertical axis roughly indicates time. Horizontal axis roughly indicates degree of difference. Point of origin of *A. roretzi* ancestral stock is unclear.

Some probable evolutionary events: 1. Character states of the ancestral stock: Male with cheliceral apophysis; male pedipalp not elongate; o.c.s. and i.c.s. strongly sclerotized; o.c.s. broad; male leg I unmodified or not strongly modified; seminal receptacles moderately well sclerotized; AL spinnerets unsegmented; burrow entrance a collapsible collar; bottom end of burrow enlarged. 2. Seminal receptacle sclerotization reduced; AL spinneret size reduced. 3. Collar becomes elongate and rigid; bottom end of burrow narrowed. 4. Male cheliceral apophysis lost; male leg I becomes more strongly modified; AL spinnerets lost. 5. Male cheliceral apophysis lost; o.c.s. narrows; male leg I increasingly modified (?); AL spinnerets lost. 6. Male leg I becomes strongly modified. 7. AME diameter reduced; male pedipalp elongate; o.c.s. and i.c.s. sclerotization somewhat reduced; male leg I modifications reduced; reduction of IVCT number. 8. AME diameter further reduced; male pedipalp further elongated; o.c.s. and i.c.s. sclerotization further reduced; seminal receptacle sclerotization reduced.

General zoogeographic considerations. The present day geographic distribution of *Antrodiaetus* and *Atypoides* (Map A) is markedly disjunct, with the greatest species diversity in far western North America. The disjunct east Asian, western North American, and eastern North American pattern and the present intimate association of these genera with the modern forest derivatives of the Arcto-Tertiary Geoflora, indicate that *Antrodiaetus* and *Atypoides* have evolved along with this well-documented (Axelrod, 1960) plant assemblage. The much greater present diversity of the Antrodiaetidae in North America indicates that this continent is probably the geographic origin of the family and of its genera. This was also Pocock's (1903) interpretation. Although the present day mecicobothriid distribution seems to support this idea, the Atypidae, with both its genera occurring in the Tropics and subtropics of the Old World (*Atypus* is also found in the Palearctic and Nearctic regions), could have originated there. This and the presence of the evolutionary relict, *Antrodiaetus roretzi*, in warm temperate Japan weakly hint that extinction could be camouflaging an Asian origin of the *Antrodiaetus-Atypoides* ancestral stock.

DISPERSAL ABILITY AND BARRIERS

Although many araneomorph spiders balloon, it is generally believed that few mygalomorph species do. I am aware of only three observations of possible *pre*-ballooning behavior in mygalomorph spiderlings: Main (1957b) and Baerg (1928) on two ctenizid species, and Enock (1885) on the atypid, *Atypus affinis*. None of these observers actually saw ballooning.

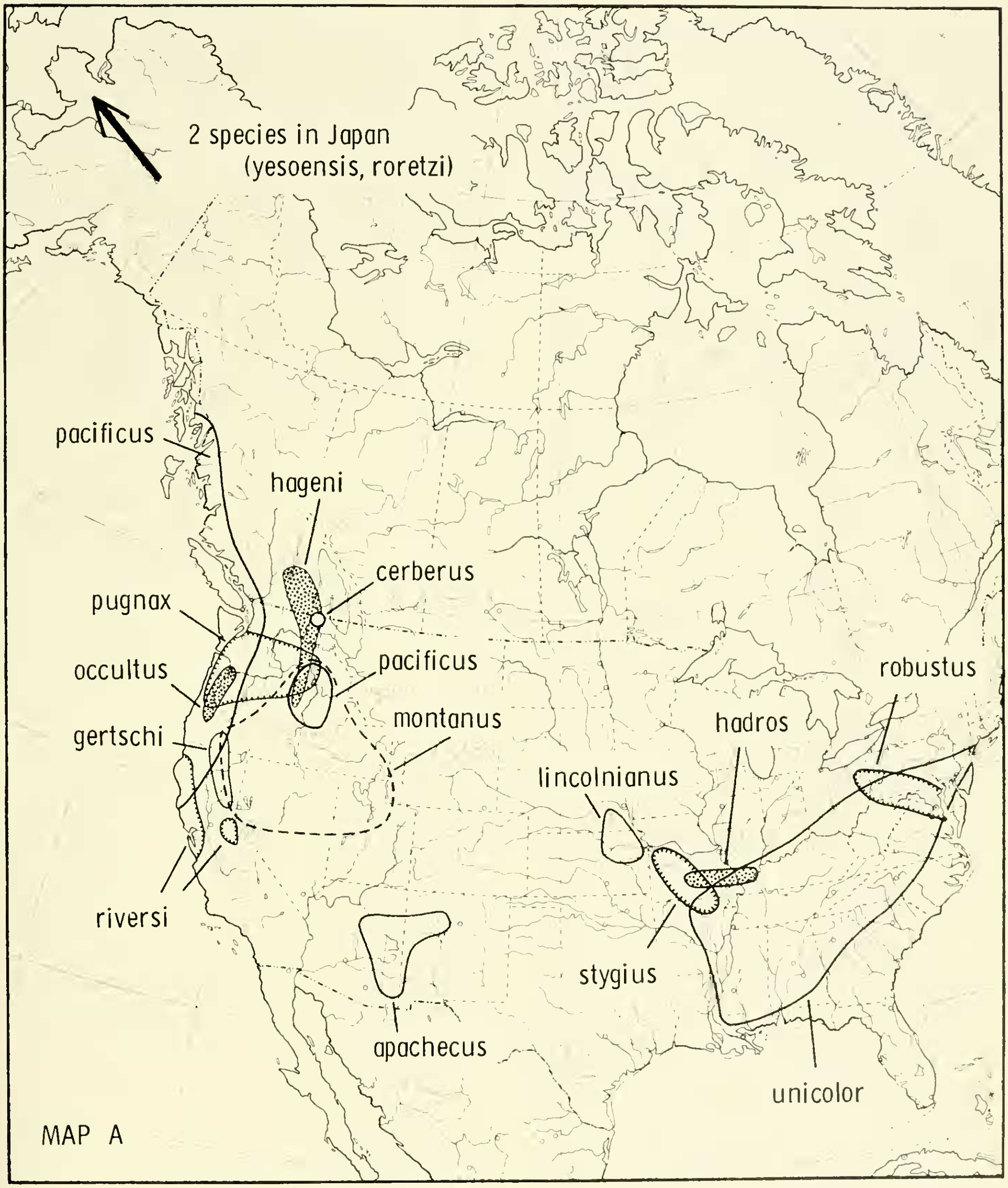
Antrodiaetus and *Atypoides* spiderlings have not been observed during dispersal away from the parental burrow, but some indirect evidence indicates that if they balloon at all, only short distances can be covered. Second instar spiderlings (the dispersal stage) desiccate quickly when not maintained in high humidity. Antrodiaetid species have considerably smaller geographic ranges than do many araneomorphs that are known to balloon. Several species exhibit marked geographic variation within relatively very small areas. Few to many offspring burrows are commonly clustered close to the parental burrow, indicating that at least some spiderling dispersal is short range.

Active dispersal of older immatures and adult females is probably prompted only by burrow microhabitat deterioration and is certainly short range. Passive rafting down streams, rivers, and perhaps across large bodies of water are likely, for burrows commonly occur within dense root systems at the bases of trees, in partly decaying logs, and near water. The colonization of the British Columbia coast and its islands by *Antrodiaetus pacificus* since the retreat of the Wisconsin ice might be largely the result of such rafting. The nocturnally wandering adult males can move rapidly (and probably far) over the ground surface. Such wandering cannot alone found new populations, but is certainly important in maintaining gene flow and probably also in fertilizing founder females in nearby localities.

Low humidity habitats (with soil humidity the immediate limiting factor) are apparently the outstanding barriers to dispersal and thus to gene flow in *Antrodiaetus* and *Atypoides* species. Geographic gaps and genetic variation discontinuities within a species population predominantly coincide with habitats drier than those occupied by the species in question. None of the likely means of antrodiactid dispersal could bridge more than a narrow dry habitat barrier.

GEOGRAPHIC VARIATION

All relatively well-sampled species of *Antrodiaetus* and *Atypoides* exhibit geographic variation in numerous characters. Five of these species (*Antrodiaetus unicolor, Antrodiaetus pacificus, Antrodiaetus pugnax, Atypoides riversi*, and *Atypoides gertschi*) exhibit strong and sometimes discontinuous geographic variation in at least several characters. The reader is referred to the Taxonomy section and to Coyle



Map A. Approximate known distribution ranges of *Antrodiaetus* and *Atypoides* species.

(1968), where a description and discussion of the geographic variation in each of these species follows each species description. Different characters frequently show similar patterns of geographic variation in each of these species, i.e., they vary concordantly. Therefore divergent populations are often defined by several characters. In some cases—particularly in *A. unicolor, A. pugnax,* and *A. gertschi*—geographically and genetically intermediate populations are known and more will probably be discovered. The clearest cases of incipient speciation (perhaps speciation is complete?) are found in *A. pacificus* and particularly *A. riversi*, where the geographic barriers to gene flow also appear most formidable. Interestingly, the predominant pattern of geographic variation in *A. pugnax* may be largely the result of character displacement, i.e., the selection pressure resulting from competition or mating errors with *Antrodiaetus occultus* in the area of sympatry may have accelerated the genetic divergence of (probably) poorly connected *A. pugnax* gene pools.

The date of disjunction (and thus the rate of phenotypic divergence) can be roughly estimated for only a few divergent populations. It is nearly certain that Pleistocene climatic fluctuations isolated the present divergent populations of *A. unicolor*, *A. pacificus*, and *A. riversi*. These disjunctions probably occurred as recently as the end of the last glacial maximum (see below); perhaps these divergent gene pools have been evolving as separate entities for as little as 15,000 years.

In each of the above five species there is greater geographic variation per unit area than in many well-studied araneomorph species. Presumably, two important factors contributing to this situation are the somewhat narrow habitat requirements and particularly the poor, long range dispersal ability of antrodiaetids. The former factor favors population fragmentation and the latter a slow rate of gene exchange among such fragments. There is some indication that burrowing mygalomorph spiders may in general exhibit much geographic variation per unit area for perhaps these same reasons (see for example Main, 1957a; Loksa, 1964; Forster and Wilton, 1968).

SPECIATION: PROBABLE HISTORICAL EVENTS

Unicolor group of Antrodiaetus. Probably the last connection between eastern and western North American populations of this species group was severed in the late Tertiary during the formation of the broad semi-arid grassland of central North America. (Map A should serve as a reference throughout this section.) It is likely that one species disjoined in this manner was morphologically and ecologically similar to, and a direct ancester of, both *A. pacificus* and *A. unicolor* (and perhaps *A. robustus*) and that therefore relatively little phenotypic divergence has occurred between these species over the last 10 to 25 million years. More recent east-west contact, such as during the cool, moist, glacial maxima of the Pleistocene, appears less likely. Present evidence indicates the absence of any widespread Pleistocene forest on the Great Plains, and that probably even narrow forest corridors allowing east-west dispersal of humid forest animals were nonexistent (Dillon, 1956; Frey, 1965; Wade, 1966). However, some controversy exists regarding this last conclusion (Blair, 1965).

The last Bering land bridge favorable for *Antrodiaetus* dispersal existed no more recently than Miocene or perhaps Pliocene times. Pleistocene Bering bridges were unforested (Simpson, 1947; Flint, 1957; Péwé, Hopkins, and Giddings, 1965), but favorable Arcto-Tertiary forest extended across the bridge during its frequent and lengthy exposures from Eocene into at least Miocene times (Simpson, 1947, Axelrod, 1960). *A. yesoensis* is probably descendant from a population that extended west from North America when the bridge was last favorable ecologically. An east to west dispersal is inferred because all other *unicolor* group species are presently North American. Thus the evidence for disjunction time of all three geographic fragments of the *unicolor* group indicates that this species group had originated by early Pliocene. The presence of the evolutionary relict, *A. roretzi*, in Japan indicates another connection over perhaps an earlier Tertiary bridge.

The relatively great diversity of *unicolor* group species in the Pacific Northwest, the marked geographic variation in certain of them, and the strong habitat differences among some of them are perhaps largely attributable to the remarkable past physiographic, climatic, and thus ecological fluctuation in this region (Detling, 1968), and to the great diversity of these factors at any one time. Such fluctuation should favor speciation by causing expansions, shifts, contractions, and disjunctions of populations. Habitat diversity and fluctuation have perhaps accelerated the genetic divergence of disjunct gene pools and favored shifts into different habitat niches. It is unclear whether most of this speciation occurred during the Pleistocene or late Tertiary.

A possible case of incipient speciation exists in *A. pacificus*, which consists of a widespread coastal population and a possibly disjunct interior montane population. At least the Oregon-Washington portion of this interior population has undergone much genetic divergence since the reduction of gene exchange with the coastal population. The barrier to gene flow between these two forest populations is the broad arm of dry Juniper-sagebrush woodland plant formation (Detling, 1968) extending northward from the Great Basin through central Oregon and Washington into southern British Columbia. Gene flow reduction and resulting genetic divergence probably began with the climatic drying and warming just after (about 15,000 years ago) the last Wisconsin glacial advance. During this maximum, a boreal forest favorable for *A. pacificus* extended at least along the ice front from the Washington coast to the mountains of northern Idaho and possibly even extended across the Oregon plateau to connect directly the coastal and northeast Oregon populations (Heusser, 1960; Detling, 1968). If the interior population is now reproductively isolated, then disjunction and speciation could also have occurred earlier in the Pleistocene under similar conditions. It is noteworthy that this distribution pattern and probably the historical causes are very similar to those of the salamanders *Plethodon vandykei* (Highton, 1962; Wade, 1966) and *Taricha granulosa* (Riemer, 1958).

Antrodiaetus unicolor is a widespread species consisting of a dense, roughly continuous central population and numerous geographically semi-isolated (some perhaps isolated) peripheral populations. Presumably the eastern, southern, and western peripheral populations were continuous with the central population during the cooler, more humid Pleistocene glacial maxima when the favorable cool humid forest habitat expanded outward over the lowland areas. Some of these peripheral populations have since undergone considerable genetic divergence as a result of the increasing discontinuity of favorable habitat peripherally and the resulting reduction of gene influx from the central population.

Lincolnianus group of Antrodiaetus. The morphologically very similar *A. stygius* and *A. apachecus* are almost certainly sister species. Perhaps the parent population split into eastern and western fragments during the formation of the grassland in the late Tertiary, the same event postulated to have last disjoined the *unicolor* group. However, the small amount of phenotypic divergence of these two species suggests a more recent disjunction during a Pleistocene interglacial. Blair (1958, 1965) has suggested this for two southwestern montane relict species of lungless salamanders, but there is considerable evidence against an east-west Pleistocene forest corridor (Frey, 1965; Wade, 1966). Pollen analysis evidence for an extensive Parkland-yellow pine association extending eastward from Arizona well into Texas at the Wisconsin maximum (Martin and Mehringer, 1965) adds some support for a possible Pleistocene connection.

Antrodiaetus apachecus is presently fragmented by intervening arid habitats into a number of disjunct montane populations that have been sampled too poorly to indicate how much they have diverged from one another genetically. These were probably last continuous near the end of the Wisconsin glacial maximum roughly 17,000 years ago when all known present populations were apparently connected by habitats no dryer than Ponderosa (yellow) pine forest (Martin and Mehringer, 1965).

Atypoides. Disjunction of *Atypoides* into eastern and western North American segments occurred at least as long ago as the formation of the late Tertiary grassland. *A. riversi* reveals a pattern of incipient speciation (Perhaps speciation is complete?) with two probably disjunct and genetically quite divergent populations on both sides of the dry Central Valley of California. These were last connected by gene flow across the valley floor (or perhaps to the north of the valley) during one of the cooler, moister Pleistocene glacial maxima, perhaps during the recent (Wisconsin) one. Similar histories have been postulated for cognate populations of salamanders with similar distributions (Stebbins, 1949; Riemer, 1958).

Reproductive Isolating Mechanisms

I should emphasize that although the study of geographic variation and the foregoing discussion may help in understanding geographic isolate formation in these spiders as well as the rate of phenotypic divergence of such isolates, nothing can be inferred about the time required for the evolution of reproductive isolating mechanisms, the crucial part of speciation.

More data is needed on the relative importance of different reproductive isolating mechanisms in antrodiaetid species. Field observations suggest that ecological isolating mechanisms are important in some sympatric *unicolor* group species in the Pacific Northwest. Temporal (seasonal) isolation exists between *A. lincolnianus* and *A. stygius* and is suggested for other species. The importance of ethological isolating mechanisms may be suggested by the species specific morphology of the male first leg of *Antrodiaetus* species. The close similarity of the male palpus and of the female genitalia of all *unicolor* group species indicates that perhaps mechanical isolating mechanisms are unimportant in these species.

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